POPULATION BIOLOGY, SOCIAL ORGANIZATION AND BEHAVIOUR OF HECTOR'S DOLPHIN

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Abstract

Hector's dolphins are threatened with local extinction by entanglement in coastal gillnets. This thesis provides data on population biology, social organization and behaviour of Hector's dolphins that help assess human impacts on their populations. To estimate population growth, I integrated anatomical studies which estimated longevity and age at first reproduction, with photographic field studies which estimated reproductive rate and survival rate. Sixty incidentally caught and beach-cast dolphins were aged from the growth layers in their teeth. Maximum age was 19 years for females and 20 for males. Females gave birth to their first calf at 7 to 9 years old, and thereafter had one calf every 2 to 3 years. Population models using these data predicted maximum population growth rates of 1.8 to 4.4% per year. These rates were exceeded by the number of Hector's dolphins recently killed in gillnets in the Pegasus Bay-Canterbury Bight area. Survival rates (including gillnet mortality) estimated using photographic identification, also suggested that this population was unable to cope with recent gillnet entanglement levels. Population models using these survival rates (0.797 to 0.865 after the first year of life), even in combination with the most optimistic reproductive rates, resulted in a decreasing population. The population models were also used to explore the likely consequences of management strategies which reduce entanglement mortality. Population size and population growth rate fluctuated markedly for several decades after a significant reduction in entanglement mortality, especially if the age structure of the population was biased towards younger individuals.

A study of social organization and behaviour pointed to another potential conservation risk. The social organization of Hector's dolphins was studied using photographic identification. Each individual associated loosely with a relatively large number of others, rather than with a few close associates, and groups frequently joined other groups and exchanged members. Sequence analysis was used to classify Hector's dolphin behaviour into five categories: 'feeding', 'sexual', 'aggressive', 'play' and 'aerial', using behaviour sequence analysis. The number of sexual behaviours per individual was highest in groups of 11-15 dolphins, and tended to increase after groups came together. The fluid association patterns and increase in sexual behaviours after groups come together suggest that Hector's dolphins have a promiscuous mating system in which males search for rather than monopolize females. Such a mating system has the potential to reduce fertilization rates in areas of low abundance.

Contents

Introduction

The aim of this study of Hector's dolphin, *Cephalorhynchus hectori,* is to provide data on reproductive rates, survival rates, population growth and social organization in order to assess human impacts on the species. Studies of this type are especially important because it has become clear that Hector's dolphin populations are threatened by entanglement in coastal gillnets (Slooten and Dawson 1988 and In press; Dawson 1990). Comprehensive studies of the population biology of the species are essential for formulating rational management policies. Hector's dolphin is found only in New Zealand waters (Baker 1978; Dawson 1985), and the total population is estimated at only 3000-4000 individuals (Dawson and Slooten 1988). This adds to the urgency of developing an effective management policy based on knowledge of the population biology and social organization of the species.

There has been a great deal of interest in the population biology of cetaceans (whales, dolphins and porpoises) in recent years (e.g. Perrin et al. 1984; Reilly and Barlow 1986; Barlow and Boveng In press). These studies are of crucial importance if we are to assess the direct and indirect human impacts on their populations. The effect of removing a given number of individuals from a population clearly depends on the potential for population growth and the social organization of the species. My work on Hector's dolphins is discussed in this context, taking into consideration what is known about other cetaceans.

Human impacts on cetaceans include pollution, habitat degradation, culls, directed catches for human consumption, and by-catches in fisheries for other species (Perrin 1988). The main danger faced by large whales (e.g. sperm whales *Physeter macrocephalus*, and humpback whales *Megaptera novaeangliae)* has been overhunting (Perrin 1988). For these large whales, the conservation prospects have improved markedly during the 1980s, with a moratorium placed on commercial whaling from 1986. In contrast, the status of many smaller cetaceans has continued to deteriorate (Perrin 1988; Brownell et al. 1989). In recent years, by-catches have taken far greater numbers of cetaceans than directed catches, and most of these have been small cetaceans (Perrin 1988).

Dolphins, porpoises and other small cetaceans are not included in the International Whaling Commission moratorium, and alarming numbers are killed intentionally and as by-catch (Perrin 1988; Brownell et al. 1989; Read et al. 1988). The river dolphins face the worst situation, as they are not only caught incidentally in fishing gear but also suffer severe habitat degradation. At least two species have been reduced to only a few hundred individuals (Brownell et al. 1989).

For most small cetaceans, by-catch or 'incidental' catch appears to be the major conservation threat (e.g. Perrin 1988; Hofman 1990). Each year, hundreds of thousands of dolphins and porpoises are caught incidentally in various fisheries around the world (Perrin 1988; Brownell et al. 1989). For example, the purse seine fishery for tuna in the eastern tropical Pacific killed an estimated 129,000 dolphins in 1986 (Perrin 1988). Gillnet fisheries for salmon and squid in the North Pacific may have killed as many as 16,000 Dall's porpoises *Phocoenoides dalli* annually in recent years (Perrin 1988).

Gillnet entanglement is a worldwide and increasing conservation problem, causing the deaths of many thousands of dolphins and other small cetaceans each year (e.g. Harwood et al. 1984; Jones 1984; Harwood and Hembree 1987; Hofman 1990). Large numbers are caught in both oceanic driftnet fisheries (e.g. Jones, 1984) and coastal gillnet fisheries in which nets are generally anchored and set on the bottom to catch groundfish (e.g. Leatherwood and Alling 1985; Read and Gaskin 1988; Brownell et al. 1989).

Monofilament gillnets have become a popular fishing method only over the last 30 years, and have already done extensive damage to cetacean populations. The Gulf of California harbour porpoise *Phocoena sinus,* the rarest marine cetacean, appears to be threatened with total extinction by incidental entanglement in gillnets (Barlow 1986; Silber 1988; Brownell et al. 1989). Populations of harbour porpoise *Phocoena phocoena* (Read and Gaskin 1988), franciscana dolphins *Pontoporia blainvillei* (Brownell et al. 1989), and probably several others (Perrin 1988) are threatened with local extinction from gillnet entanglement. All four species in the genus *Cephalorhynchus*, including Hector's dolphin, are caught incidentally in gillnet fisheries (Goodall et al. 1988a, b; Baker 1978; Slooten and Dawson 1988; Dawson 1990). In addition, the two South American species *(C. commersonii*

and *C. eutropia)* are caught intentionally, for use as crab bait (Goodall and Cameron 1980; Goodall et al. 1988a, b).

Of particular concern are fisheries in which by-catch leads to directed catch. In Peru, for example, dolphins and porpoises have been caught incidentally in coastal gillnet fisheries for sciaenids and sharks since at least the 1960s (Read et al. 1988). The meat was sold locally for human consumption, and when the anchoveta fishery collapsed in the early 1970s some fishermen shifted to using gillnets to target dusky dolphins *Lagenorhynchus obscurus* and other small cetaceans. This directed fishery is thought to catch some 10,000 small cetaceans annually, and may endanger local populations (Read et al. 1988; Perrin 1988).

In many cases the impact of incidental catch on marine mammal populations is unknown (Perrin 1988; Brownell et al. 1989; Hofman 1990). Population biology and entanglement are under study for several small cetaceans, to help fill this information gap (see Perrin 1988). Before this study it was impossible to assess the impact of gillnet entanglement on Hector's dolphin populations. Besides data on population size (Dawson and Slooten 1988) and the level of gillnet entanglement (Dawson 1990), data on population growth and social organization were urgently needed.

This thesis presents data from several different fields of study. To answer the question of population growth, I integrate anatomical studies which estimate longevity and age at first reproduction (Chapters 1-3), with photographic field studies which estimate reproductive rate and survival rate (Chapter 5). Population models based on these data are used to estimate maximum population growth rates and to explore the likely consequences of management strategies which reduce entanglement mortality (Chapter 4).

I also report on studies of the social organization and behaviour of Hector's dolphins, emphasizing those aspects which provide a more complete understanding of their population biology. Individual association patterns are studied using a photographic identification catalogue (Chapter 6). Chapter 7 provides a description of the social behaviour of Hector's dolphins, and an analysis of the relationship between sexual behaviour and group dynamics.

The social organization of a species, including association patterns and social behaviour, can have important effects on life-history patterns and population biology (e.g. Bekoff et al. 1984; Schaller 1977). The interaction between social organization, life-history and population biology is of great interest to both evolutionary biologists (e.g. Horn and Rubenstein 1984; Krebs 1985; Rubenstein and Wrangham 1986) and conservation biologists (e.g. Schaller 1977; Schaller et al. 1985; Gilpin and Soulé 1986; Lande 1988). Most important for conservation biology is that social organization, especially mate searching behaviour, may affect the reproductive rate of a population and may help explain the effects of population size on reproductive rates (e.g. Whitehead 1987). The relationship between social organization and conservation biology is discussed in Chapters 3, 6, 7 and the thesis Discussion.

Division of labour in co-authored manuscripts

Chapters 4, 5 and 6 have benefitted from collaboration with other researchers. Steve Dawson took the photographs used to identify individual Hector's dolphins, and processed and printed them. I compiled the photographic catalogue and computer database containing data on where and when photographs were taken, and analyzed the data.

Frank Lad provided invaluable mathematical advice and checked the results of the population models by calculating the eigenvalue of the matrix of reproductive and survival rates directly (Chapter 4). He also contributed to Chapter 5, by suggesting I analyze the Akaroa Harbour sightings separately to estimate how many of the 'disappearances' were due to dolphins having moved outside the study area rather than died. I carried out the analysis for all chapters, including the design of the population models in Chapter 4.

Section I. Population biology

Chapter 1
Age and body length of Hector's dolphins

Abstract

Dentinal growth layers were used to estimate the ages of a sample of 60 Hector's dolphins. Seasonal trends in dentine deposition indicated that one growth layer group, consisting of one stainable and one unstainable layer, was deposited each year. The maximum observed age was 19 years for females and 20 for males. The sample included individuals of a wide range of sizes, from newborns measuring 76.6cm total length to adults of up to 144.2cm. When age was compared with body length, adult females were found to be larger than males. The traditional procedure for preparing dolphin teeth was simplified by using a faster stain and more readily available embedding and sectioning equipment. An important advantage of this method is that it makes it possible to cut thinner sections, increasing the chances of obtaining a section through the centre of the pulp cavity.

Introduction

A method of determining the age of individuals with known reproductive status is a necessity for studies of the population biology of any species. Tooth sectioning has become a standard procedure for gathering this information. A large body of research on age determination in dolphins and other odontocetes has shown that the teeth of most species have incremental growth layers in the dentine and cementum which can be used to estimate age (for reviews see Scheffer and Myrick 1980; Perrin and Myrick 1980). Unlike many terrestrial mammals, dolphins do not have deciduous teeth, and therefore their teeth contain a complete growth record.

Growth layers in mammalian dentine and cementum are visible as successive opaque and translucent layers in sectioned teeth examined in transmitted light, or as alternately stainable and unstainable layers when the section is decalcified and stained (Grue and Jensen 1979; Perrin and Myrick 1980). The incremental growth layers are laid down parallel to the pulp cavity edge at regular intervals, usually seasonally with one predominantly starting to form in summer and the other in winter. The summer layer is usually relatively wide and opaque, and stains well with histological stains such as haematoxylin and

toluidine blue, whereas the winter layer is narrower, translucent and unstainable. In most toothed cetaceans one such pair of layers, also called a growth layer group or GLG, appears to be equivalent to one year's growth (e.g. Perrin and Myrick 1980; Hohn et al. In press).

The time period represented by a GLG can be verified through investigation of the seasonality of growth layer deposition. If teeth are available from a sample of individuals who died in all or most months of the year, the type (stainable or unstainable) and rate of deposition of the last growth layer provide evidence of the time interval represented by each growth layer. This is a technique commonly used for age determination of fish which form annual growth layers in their otoliths, scales, finrays and other structures (Bagenal 1974). As appears to be the case in the teeth of most dolphins and land mammals (e.g. Klevezal 1980), fish otoliths form a wide opaque zone in summer-autumn and a narrow translucent zone in winter-spring (Liew 1974; Bagenal 1974).

The seasonal deposition pattern of growth layers has been investigated for several dolphin species, including *Tursiops truncatus* (Sergeant 1959), *Stenella attenuata* (Kasuya 1972; Kasuya et al. 1974), *Stenella coeruleoalba* (Miyazaki 1977) and *Pontoporia blainvillei* (Kasuya and Brownell 1979), for the harbour porpoise *Phocoena phocoena* (Gaskin and Blair 1977) and other marine mammals (e.g. Gambell 1977; Marsh, 1980). For most species examined, the seasonal pattern indicates that one GLG is laid down annually.

Direct evidence that one GLG is deposited each year is available from captive-born dolphins (e.g. Sergeant et al. 1973), as well as dolphins and porpoises that had been treated with tetracycline antibiotics which leave markers in growing teeth and bones (e.g. Best 1976; Gurevich et al. 1980; Nielsen 1972). Recently, Hohn et al. (In press) have confirmed that GLGs are annual in free-living dolphins by extracting teeth from known-age individuals.

In this study, seasonal deposition was used as an indicator of the time interval represented by each growth layer. The age estimates have been applied to reproductive studies (Chapters 2 and 3) and to a population model for Hector's dolphin (Chapter 4).

Methods

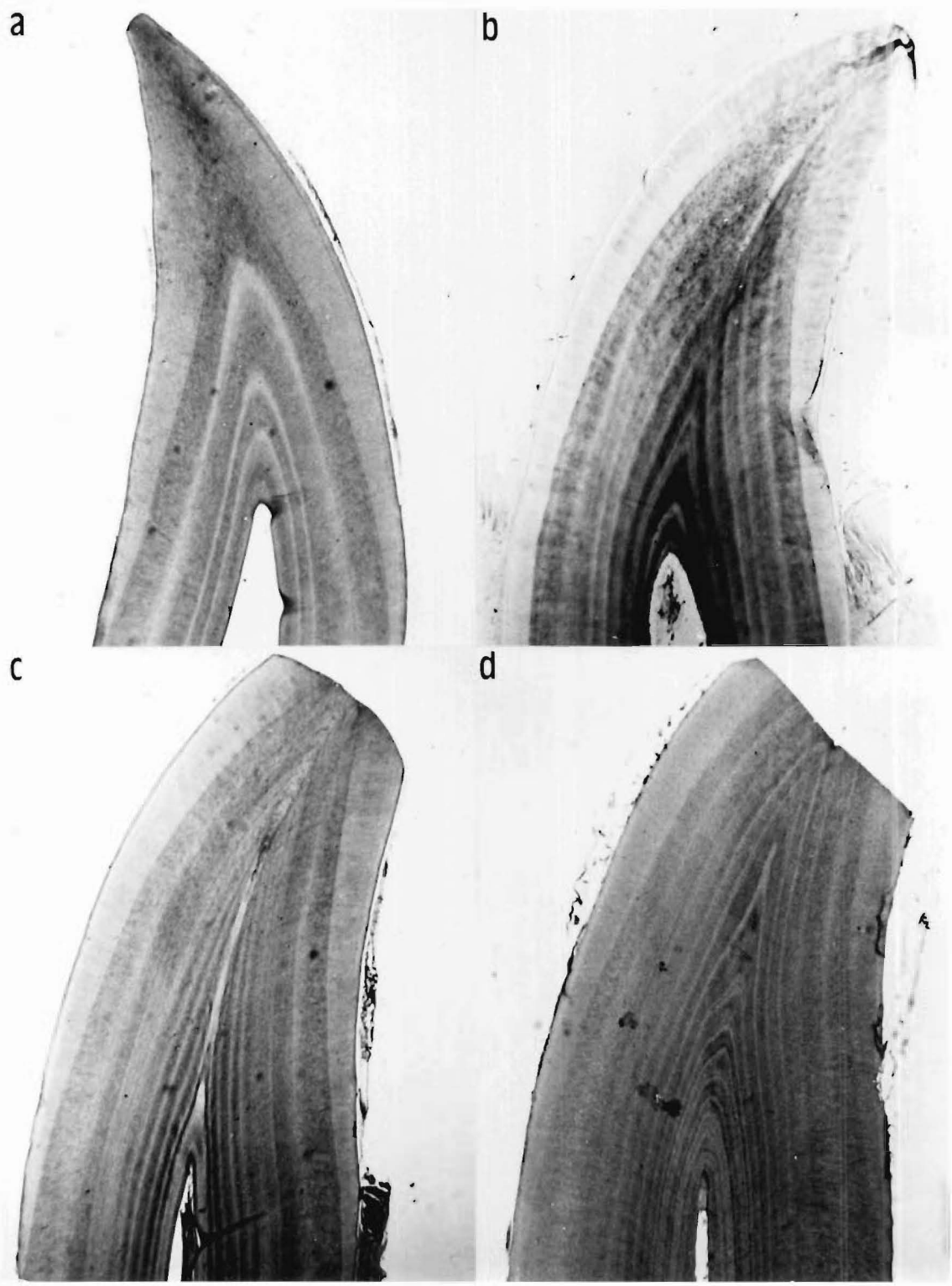
Between December 1984 and February 1989, as part of a study of the biology of Hector's dolphin, Slooten and Dawson (1988; In press) received 60 dead dolphins for examination. Of these, 43 had been incidentally caught in commercial and recreational gillnets, four caught in trawlnets and one caught in the buoy-line of a crayfish trap. The cause of death was unknown for 12 individuals. All were dead when first found, and none were killed for the purposes of this study. The sex ratio was approximately equal, with 33 females and 27 males (not significantly different from 30:30).

Hector's dolphins have up to 30 small, simple, conical teeth in each side of each jaw. Three teeth from each dolphin were selected on the basis of greatest size, least damage and least wear, and stored in 10% formalin. The teeth of adult dolphins were up to 13mm long from tip to root and 3mm in diameter at the widest part.

Teeth were decalcified in 5% nitric acid, using at least 100ml per gram of tooth. Three teeth from each individual were placed in separate plastic (tissue-processing) cassettes. These were immersed in a jar of acid which was agitated at least four times a day. Decalcification was complete after about 24 hours of immersion for juvenile teeth and up to 48 hours for teeth from old adults. After decalcification the teeth were rinsed in running tap water for at least 24 hours. Decalcified teeth were slightly flexible, and could be cut with a scalpel. About a third was cut off each tooth longitudinally to hasten the process of reaching the pulp cavity during sectioning. Still in their plastic cassettes, the teeth were then put through a standard tissue-processing and wax-embedding process as for soft tissues. The cut surface allowed better contact of the tooth tissue with processing fluids and wax, and the flat, cut surface made embedding easier. Sections were cut at 2-4μ, using a Leitz microtome and disposable blades. I used toluidine blue for staining.

Age determination was based on the number of growth layers in the dentine, counted at 40 to 100x magnification. One GLG was defined as one broad stainable layer and one narrow unstainable layer. These GLGs start after a broad layer of fetal dentine has been deposited (see Fig. 1). The type (stainable or unstainable) of the most recently forming growth layer was noted, to investigate seasonal trends in deposition rate of GLGs.

Figure 1. Examples of tooth sections from individuals aged 4 (a), 7 (b), 10 (c) and 19 years old (d), to the same magnification (scale bar=1mm). The enamel has been removed by decalcification. Starting from the outer edge of the tooth, the first layer consists of fetal dentine, laid down before birth. This layer is wide and lightly stained, intermediate in colour to the alternating dark and light layers which make up the rest of the tooth. Each GLG consists of one wide, darkly stained layer and the narrow unstained layer which follows it.


a
b
c
d

Results

The tooth cementum was thin without obvious incremental growth layers, but the dentine was clearly layered. The pulp cavity was wide and conical in young dolphins, and decreased in size with increasing age (Fig. 1). It was more difficult to obtain sections through the pulp cavity in the older individuals, but sectioning revealed an open pulp cavity in all the teeth examined. Whenever several teeth from the same individual were examined, the GLG count was the same for each tooth. The maximum number of GLGs counted was 19 for females and 20 for males.

Seasonal trends in dentine deposition indicated that Hector's dolphins form one GLG per year, consisting of one stainable and one unstainable layer. The wide, stainable layer was the innermost layer forming in the teeth from all individuals who died between February and June. Individuals who died in November and early December were forming the narrow, unstainable layer, which in most individuals was complete or very nearly so. Individuals who died in January were a mixture, with some having nearly completed the unstainable layer and some having just started the stainable layer.

Accumulation of growth layers in young dolphins provided a second check on the rate of deposition. In most dolphin species, newborns have distinctive fetal fold marks on their flanks. In Hector's dolphins these fold marks cause a change in the pigmentation of the skin, and they are visible as light-grey stripes against a darker grey background for nearly six months (Slooten and Dawson 1988). During summer, this makes it easy to distinguish individuals less than a year old from those between 1 and 2 years old. In all cases, the number of growth layers in the teeth of young, obviously first and second year individuals, was consistent with annual deposition of GLGs.

The relationship between age and body length (Fig. 2) shows that first-year individuals, between birth and 1 year old, fell into the size range 76.6 to 99cm TL (total length from snout to tail notch), and second-year individuals measured between 104.6 and 119cm TL. After the second year, body length increased more slowly, and total length became a poorer indicator of age.

Females reached a larger size than males, and Fig. 2 suggests that females are larger than males at any given age. Adult males (8 years and over)

Figure 2. Age/length distribution showing variation in size and suggesting that females are larger at all ages.

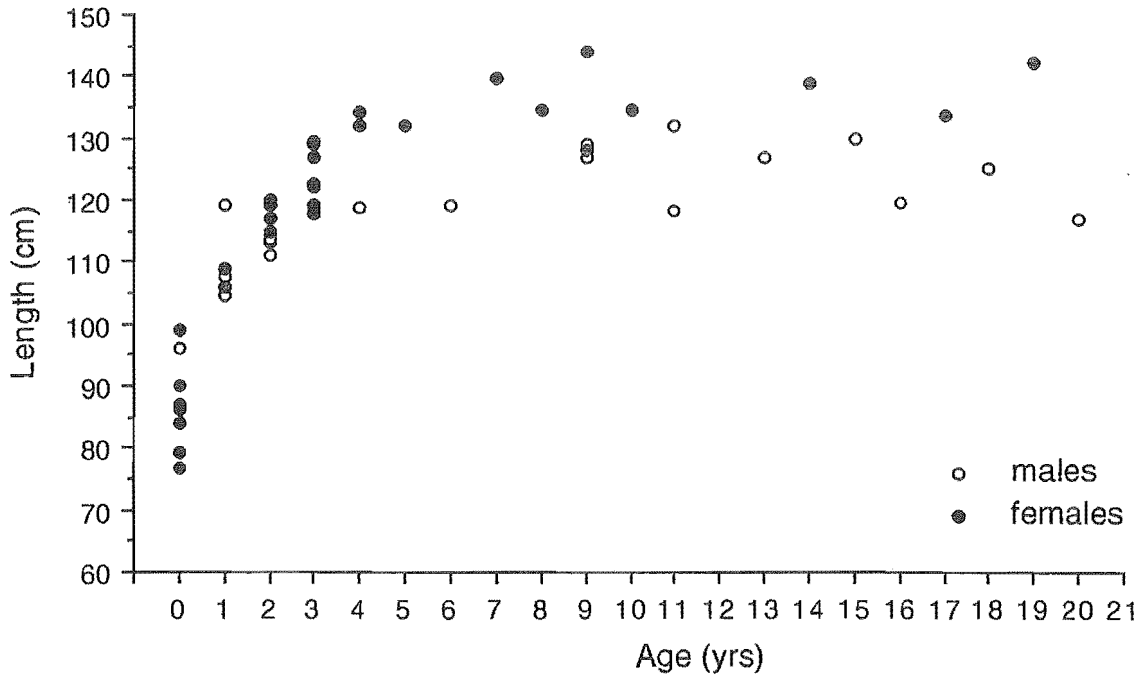
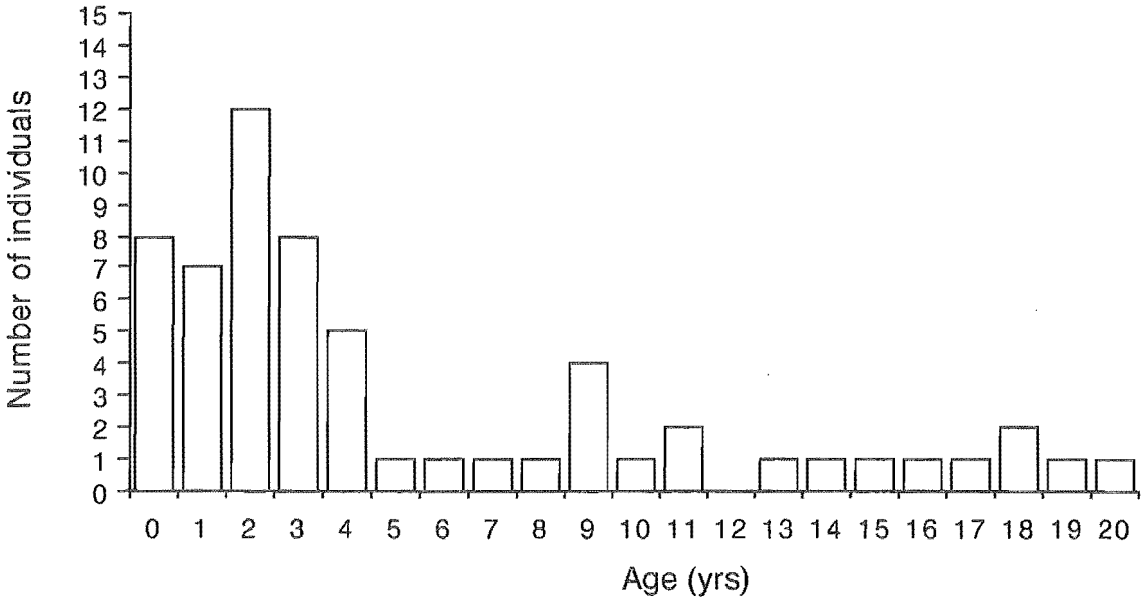


Figure 3. Age/frequency plot of the 60 Hector's dolphins examined.



averaged 125cm TL (S.D. = 5.41, n = 9), and were significantly smaller than females (t-test, p = 0.001), averaging 136.6cm TL (S.D. = 5.6, n = 7).

The age-frequency plot (Fig. 3) suggests a relative over-representation of younger individuals, especially individuals in the 2-year age class, and possibly an under-representation of individuals between 5 and 8 years old.

Discussion

The accumulation of growth layers in the dentine of Hector's dolphins follows a seasonal pattern, with a stainable layer starting to form in summer and continuing into winter, and an unstainable layer completed in spring. This is similar to the seasonal accumulation pattern found in other small cetaceans from the Southern Hemisphere, for example *Pontoporia blainvillei* (Kasuya and Brownell 1979) and *Cephalorhynchus commersonii* (Lockyer et al. 1988), and from the Northern Hemisphere, for example *Stenella attenuata* (Kasuya et al. 1974) and *Phocoena phocoena* (Gaskin and Blair 1977). Like most other researchers (e.g. Kasuya and Brownell 1979; Lockyer et al. 1988; Hohn et al. In press), I have concluded that a GLG consisting of one stained and one unstained layer equates to one year's growth.

The smallest individual examined was 76.6cm in total length, and still had a small piece of attached umbilicus. Birth size for *Cephalorhynchus commersonii* has been estimated at 75-80cm (Goodall et al. 1988a), and is likely to be similar for *Cephalorhynchus hectori*. As in *C. commersonii*, the curve of age versus body length for *C. hectori* indicates a marked slowing of growth at about 5 years; a phenomenon often associated with sexual maturation. Female Hector's dolphins give birth to their first calf between ages 7 and 9, and appear to begin ovulation at 6 years at the earliest (Chapter 2). Males apparently mature between the ages of 6 and 9 (Chapter 3). After the first 2 or 3 years, body length is a rather poor indicator of age, due to the large amount of variation in body length at any given age.

Female Hector's dolphins grow to a greater total length than males, as do the females of most small dolphins and porpoises including Commerson's dolphin *C. commersonii* from South America (Goodall et al. 1988a) and from the Kerguelen Islands (Collet and Robineau 1988), franciscana dolphin *Pontoporia blainvillei* (Kasuya and Brownell 1979), and harbour porpoise

Phocoena phocoena (Gaskin and Blair 1977). In general, females are larger than males in the baleen whales, and males are larger in the toothed whales. The smallest toothed whales seem to be an exception to this general rule.

Ralls (1976) noted that females are larger than males in more species of mammals than is generally supposed. She concluded that this is not correlated with female dominance or polyandry, but that large females tend to be larger in species in which the lack of some resource is more critical to the reproductive success of females than of males. Ralls (1976) suggested that competition among females would lead to greater female size and a higher mortality rate among females.

The toothed whales have relatively large offspring for the size of the adult, and the relative size of newborns tends to increase with decreasing adult size of the species (Ralls 1976). Therefore, an alternative explanation would be that there is a minimum size below which newborn dolphins are unable to survive, perhaps for thermal reasons, and a minimum size below which female dolphins and porpoises are unable to reproduce and care for their calves successfully. It is interesting that the males of these species are smaller than the females, considering they have relatively large testes and that the mating system is probably polygynous or promiscuous (see Chapter 3).

The maximum observed age of 20 years for *C. hectori* is similar to that of other small cetaceans. *Cephalorhynchus commersonii*, the only other species in this genus for which such information is available, has a maximum observed age of 18 years (Lockyer et al. 1988). It is possible that older individuals of both species will be found in a larger sample of aged individuals. However, the maximum age estimate for *Cephalorhynchus commersonii* increased only from 17 to 18 with a sample-size increase from 40 (Lockyer et al. 1981) to 136 aged individuals (Lockyer et al. 1988). *Pontoporia blainvillei,* another small dolphin, has a maximum observed age of 16 years (Kasuya and Brownell 1979). Among the porpoises, *Phocoena phocoena* lives to around 15 years and *Phocoenoides dalli* to 16-18 years (Gaskin et al. 1984). The larger dolphins, with body lengths in the range of 1.8-3m appear to have much longer life-spans, between 25 and 50 years (Perrin and Reilly 1984).

I have not tried to estimate survival rates from the age distribution of this sample of Hector's dolphins. The assumption of a stable population which is

neither growing nor declining is unlikely to be satisfied as Hector's dolphin populations have been subject to widely varying levels of gillnet entanglement (see Dawson 1990). In addition, the entangled and beach-cast dolphins examined may not represent a random sample of the population. The age distribution of the sample suggests an over-representation of young individuals, and the same pattern is shown when gillnet-caught dolphins are separated from beach-cast individuals (see Chapter 4 and Dawson 1990). Interestingly, 2-year-olds seem particularly over-represented in the Hector's dolphin sample. This corresponds to the approximate age when a young dolphin is no longer constantly accompanied by its mother. It is possible that certain age groups either encounter gillnets more often than others, or are less able to detect gillnets or escape from them once caught.

It is not uncommon for even very large samples of incidentally caught dolphins to show an unusual age distribution. Sampling bias, rather than a non-stable age distribution, was thought to be a more likely explanation of the marked deficiency of individuals from 5-15 years old in a large sample of spotted dolphins *Stenella attenuata* killed in the eastern Pacific tuna purse-seine fishery (Barlow and Hohn 1984).

Most researchers working with decalcified teeth use a freezing microtome to cut sections at 15-20μ thickness (e.g. Lockyer et al. 1981, 1988; Perrin and Myrick 1980). Others grind sections to 20-30μ before decalcification (e.g. Kasuya and Brownell 1979). These sections are usually stained with haematoxylin for 30 to 90 minutes (e.g. Scheffer and Myrick 1980; Myrick et al. 1983). In contrast, very good results were obtained with the Hector's dolphin tooth sections by sectioning at 2-4μ and staining in toluidine blue for just one minute. Toluidine blue is a readily-available stain which does not require ripening. The results presented here show that it is possible to simplify the processing of dolphin teeth considerably by using a faster stain, and a standard microtome which is more readily available than a freezing microtome. An advantage of thin sectioning is that it increases the chances of obtaining a section through the centre of the pulp cavity. In addition, the block can be easily stored for further sectioning if necessary. Modern techniques of plastic embedding would be well worth investigating as the plastic polymers used are more similar in hardness to tooth tissue than the wax used in standard histology.

Chapter 2
Changes in the ovaries and uterus of Hector's dolphins with age and reproductive activity

Abstract

Accurate estimates of reproductive parameters are essential for rational conservation management of Hector's dolphin populations. This chapter reports the results of a detailed macroscopic and histological study of reproductive tracts from females found beach-cast or killed incidentally in fishing gear. In Hector's dolphins, *Cephalorhynchus hectori*, corpora albicantia remain visible at least until the next ovulation, and likely for the lifetime of the female. With an average age at first reproduction of 7 to 9 years, a maximum age of around 19 years and a calving interval of 2 to 3 years, female Hector's dolphins could produce a maximum of four to seven calves per lifetime.

Introduction

Hector's dolphin is a small, inshore species, endemic to the waters around New Zealand, with an estimated total population of 3000-4000 individuals (Dawson and Slooten 1988). The species has recently suffered an alarming level of incidental entanglement in gillnets (Slooten and Dawson In press; Dawson 1990; Marine Mammal Commission 1988, 1989). Until recently, the development of effective conservation and management programs for Hector's dolphin has been impeded by a paucity of data on its reproductive biology.

Detailed macroscopic and histological examination of the ovaries of a large variety of cetaceans have been made in order to study their reproductive biology and life history (Best 1967; Collet and Harrison 1981; Harrison et al. 1969, 1972, 1981; Harrison and Brownell 1971; Harrison and Ridgway 1971; Lockyer 1987; Marsh and Kasuya 1984; Perrin et al. 1984). The data gathered have often been used to estimate acceptable levels of human impact on the species from directed or incidental catches (e.g. Lockyer 1984; Braham 1984, and other papers in Perrin et al. 1984).

The aim of this study was to provide estimates of reproductive parameters necessary to guide conservation management of this species, particularly age

at sexual maturity, age at first reproduction and reproductive rate. These estimates have been used to construct population models for Hector's dolphin (Chapter 4).

Methods

The reproductive tracts of 33 female Hector's dolphins were examined. A schedule of external measurements (modified after Norris 1966) and measurements and weights of internal organs was taken for each dolphin. The internal organs, and any samples suspected of pathology or parasitic infestation, were passed on to parasitologists at Canterbury University and the Lincoln Animal Health Laboratory (Ministry of Agriculture and Fisheries). Stomach contents and skeletons were retained, as well as teeth for age determination (Chapter 1). The ovaries of one of the females were damaged. This female was excluded from the analysis, because her reproductive status could not be determined with certainty.

During the dissections, reproductive tracts and ovaries were removed, measured with vernier calipers, photographed, and stored in 10% formalin. After storage, histological sections were taken midway along each uterine horn, and the whole uterus was opened and checked for embryos. The uteri were also checked for serosal stretch marks which are an indication of previous pregnancy (Benirschke et al. 1980). Mammary glands were examined, measured (and weighed if possible) and samples were preserved in formalin.

After storage in 10% formalin, the ovaries were blotted dry and weighed to the nearest 0.1g and examined carefully for the presence of any corpora lutea (CLs) and corpora albicantia (CAs). Each pair of ovaries was photographed and the CLs and CAs were marked and numbered on the photographs. After macroscopic external examination, samples of the corpora were taken for histology, and their diameters measured to the nearest millimetre in three planes. The ovaries were then sliced into 1mm thick slices, to check whether any corpora or pathologies had been missed. Histological preparations were made of each CA and CL. These samples were embedded in paraffin, sectioned, and stained with haematoxylin and eosin.

In this chapter, regressing and regressed corpora lutea (CLs) are referred to as corpora albicantia (CAs) irrespective of their colour. Three stages in the size and histological appearance of CAs were observed, which were assumed to relate to their age. CAs were classified as large, medium or small according to the following criteria (adapted from Marsh and Kasuya 1984). Regression appears to be a continuous process, and these categories are somewhat arbitrary, but they provide a useful guide to the state of regression.

Large CAs (mean diameter: 7 to 10mm) were clearly visible on the surface of the ovary as a raised, spherical knob or raised wrinkled scar, with an obvious stigma. In large CAs, most luteal cells had been replaced by cellular fibrous tissue, but remnants of luteal cells were still present in very large, young CAs. The fibrous connective tissue had become progressively more acellular as fibroblasts produced more extracellular fibres. Very young CAs were still highly vascular, but in most large CAs relatively acellular connective tissue formed the bulk of the structure.

Medium CAs (mean diameter: 3.5 to 7mm) protruded from the ovary surface no more than half as much as large CAs, and were visible as a raised, wrinkled scar. In medium CAs, much of the fibrous tissue had disappeared, causing blood vessels to become a more obvious part of the structure. Fibrous tissue and blood vessels were present in roughly equal amounts.

Small CAs (mean diameter: 1 to 3.5mm) were visible on the ovary surface as a small wrinkled scar, barely protruding from the ovary surface. In small CAs, the fibrous connective tissue had become very reduced and almost disappeared, with blood vessels lying close together and forming the bulk of the structure.

Sexual maturity is generally defined as the age at which a female has ovulated at least once, as evidenced by the presence of at least one corpus luteum or corpus albicans in the ovaries (Perrin and Reilly 1984). This definition assumes that corpora albicantia remain visible in the ovaries indefinitely, or at least until the next ovulation. Evidence that this is a reasonable assumption is given below.

Results

Of the 32 females examined, 25 were immature with small, undeveloped ovaries and uteri. The remaining 7 females had ovaries with CAs (Table 1) and uteri with serosal stretch marks, indicating they were sexually mature and had been pregnant at least once (Benirschke et al. 1980). Thus, for each of the three females with only one CA the first ovulation resulted in a pregnancy. Two of these females were lactating heavily at the time of death, and all evidence suggests that these two females gave birth following their first ovulation. None of the immature females had serosal stretch marks (see Fig. 1 for appearance of mature and immature reproductive system). All females 5 years old and younger were immature, while those 7 years and older had ovulated and been pregnant at least once.

The ovaries of immature Hector's dolphins were flat and oval with smooth surfaces, measured from 1.4 x 0.7 x 0.3mm to 2.9 x 1.3 x 0.7mm, and weighed from 0.2 to 2g. They increased in size and thickened with age (Fig. 2). The ovaries of the 6-year-old female contained many large antral follicles, but no evidence of ovulation.

In Hector's dolphin, follicle growth and the development of CLs and CAs apparently follow the usual pattern for cetaceans (Perrin and Donovan 1984) and other mammals (Peters and McNatty 1980). Large follicles were readily visible macroscopically, and the largest ones showed as bulges on the surface of the ovary. CAs were visible as raised, spherical knobs (large CA) or wrinkled scars (medium and small CA) on the ovary surface. The large CAs had a clearly defined stigma, indicating the rupture point of the mature follicle which gave rise to it. All CAs detected were visible on the ovary surface, and no additional corpora were found by sectioning.

Two large CLs were found, both of which were apparently CLs of pregnancy. The smallest, measuring 22x16x17mm, was found in the left ovary of the 17-year-old female, and consisted of the typical large, rounded luteinized cells. This female was pregnant, with a small embryo (12x5.8mm max. width and length, approx. 4-5 weeks old) in the left horn of the uterus. The largest CL was found in the left ovary of one of the 9-year-old females, and measured 26.1x21x19mm. In this CL a small proportion of the luteinized cells had been replaced by collagen. The uterus size and histology indicated that this female

Figure 1. External appearance of the reproductive tract of immature females (a, b) and mature females (c, d), showing the ovaries at each end of the two-horned uterus and stretch marks on the uteri of the mature females (scale bars=20mm). The largest uterus in the sample (d) belonged to a female who appeared to have recently aborted a half-term fetus (see section on pathologies).

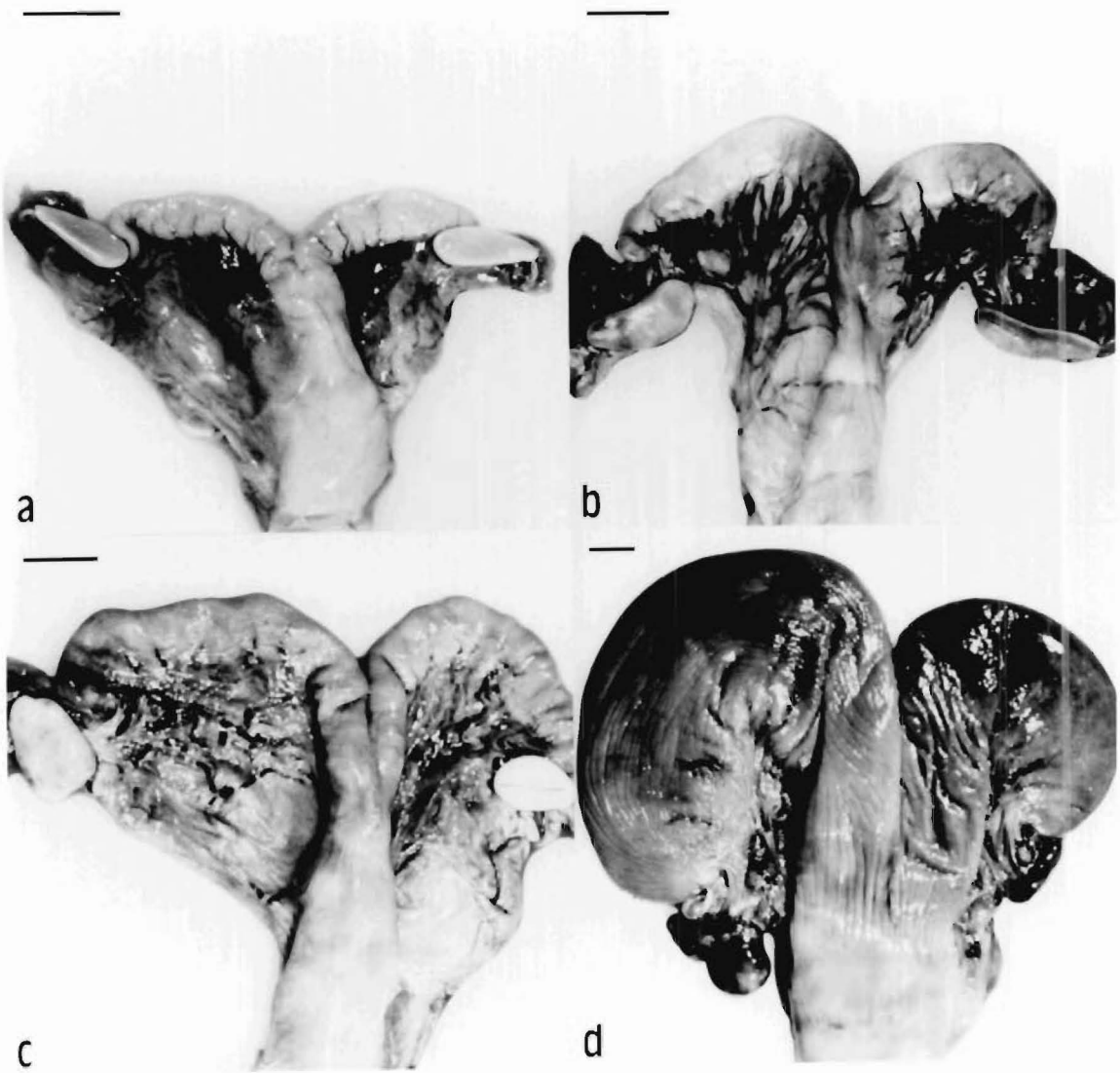

a
b
c
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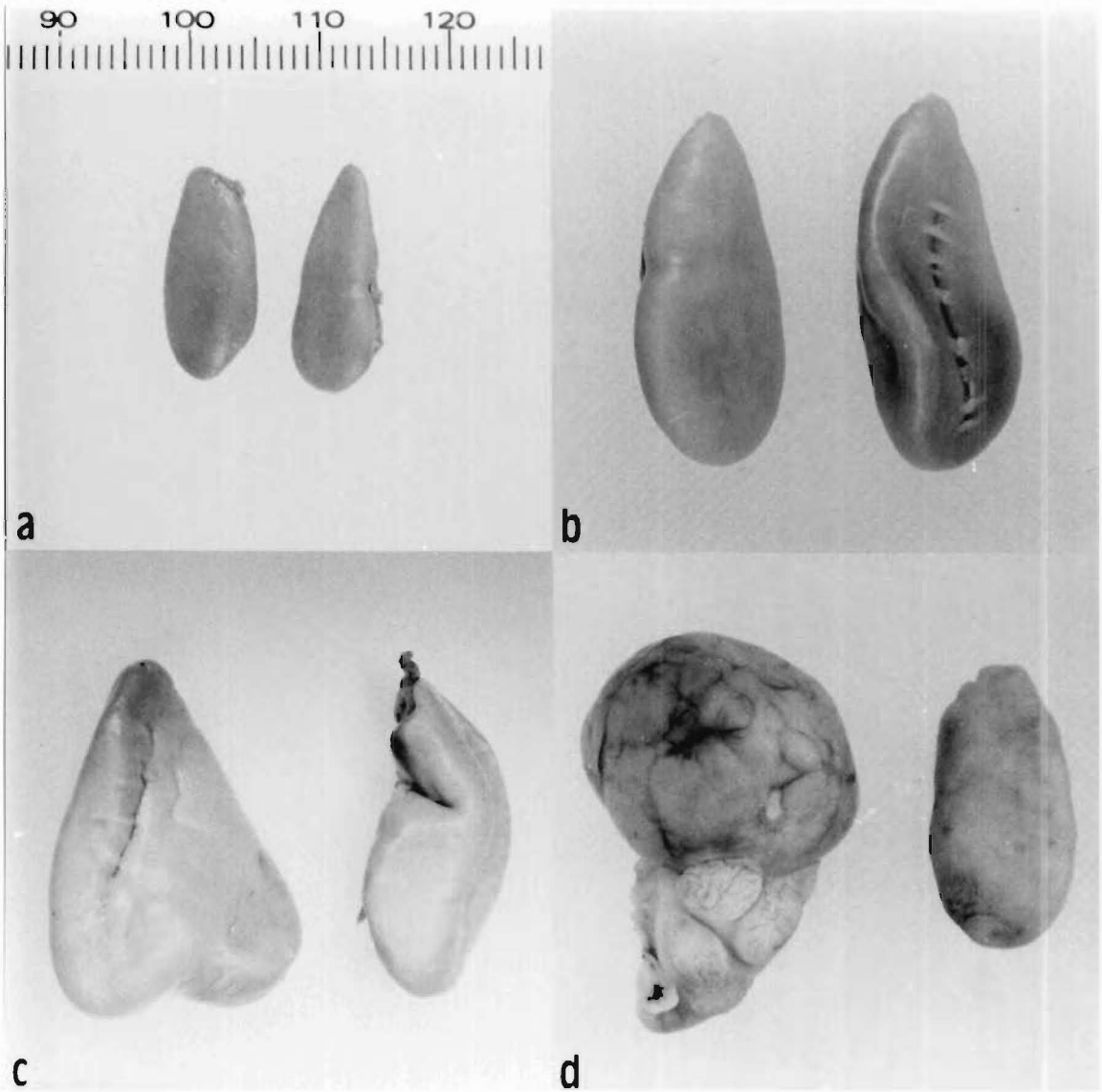
Table 1. Individual and reproductive characteristics of female Hector's dolphins. Wt = weight; CAs = corpora albicantia; CLs = corpora lutea, Diam. = flat diameter; Endom. = endometrium condition: Im = immature, MA = mature-anoestrus, ML = mature-lactating, F = follicular, P = pregnant; AFR = age at first reproduction.

Age	Length	Weight	Month	Left ovary			Right ovary			Left uterine horn		Right uterine horn		Lactating	AFR
(yrs)	(cm)	(kg)	of death	Wt (g)	CAs	CLs	Wt (g)	CAs	CLs	Diam.	Endom.	Diam.	Endom.		
0	76.6	9.5		0.3	0	0	0.2	0	0	1.0		1.0		n	
0	79.2	11.3	Dec	0.3	0	0	0.2	0	0					n	
0	84.0	13.5	Dec	0.3	0	0	0.3	0	0	1.1		1.3		n	
0	86.0	11.3	Dec		0	0		0	0					n	
0	87.0	11.0	Jan		0	0		0	0					n	
0	90.2	15.6	Feb	0.4	0	0	0.4	0	0	1.0		1.1		n	
0	99.0	23.5	Apr	0.7	0	0	0.7	0	0	1.1		1.0		n	
1	106.0	25.7	Nov	0.4	0	0	0.4	0	0	1.3		1.4		n	
1	109.0		Feb		0	0		0	0					n	
1			Jan		0	0		0	0					n	
2	115.0	27.5	Feb	0.3	0	0	0.3	0	0	1.1		1.1		n	
2	117.2	28.5	Dec	0.3	0	0	0.4	0	0	1.3		1.4		n	
2	119.0	18.0	Apr		0	0		0	0					n	
2	120.0	21.0	Feb	0.8	0	0	0.8	0	0	1.3	Im	1.3	Im	n	
2	120.0	29.9		0.8	0	0	0.7	0	0	1.4	Im	1.3	Im	n	
3	118.0	31.0	Jan	0.5	0	0	0.5	0	0	1.4		1.3		n	
3	119.0	26.6	May	0.7	0	0	0.7	0	0	1.2		1.4		n	
3	122.5	32.0	Nov	0.5	0	0	0.5	0	0	1.3	Im	1.3	Im	n	
3	127.0	33.0	Jan	0.7	0	0	0.7	0	0	1.6		1.5		n	
3	129.0	37.0	Jan	1.1	0	0	1.3	0	0	1.4	Im	1.3	Im	n	
3	129.5	37.5	Jan	1.2	0	0	1.1	0	0	1.5		1.6		n	
4	132.0	41.5	Jan	1.2	0	0	1.3	0	0	1.4		1.4		n	
4	134.0	35.4	Dec	0.6	0	0	0.6	0	0	1.7		1.7		n	
4	134.0	38.0	Jan	0.7	0	0	0.5	0	0	1.5	Im	1.6	Im	n	
5	132.0	42.0	Dec	1.2	0	0	1.2	0	0	1.8		2.2		n	
7	139.6	47.0	Jan	2.5	1	0	1.3	0	0	2.3	ML	2.5	ML	y	7
9	128.0	43.0	Dec	2.7	1	0	1.1	0	0	2.1	MA	2.0	MA	n	8-9
9	144.2	48.0	Jun	14.4	6	1	1.9	0	0	7.5	P	9.5	P	n	?
10	134.6	40.8	Oct	3.2	1	0	1.3	0	0	1.9	F	1.9	F	y	8-9
14	139.0	44.0		2.1	4	0	0.9	0	0	3.4	MA	2.8	MA	?	?
17	133.6	45.5	Dec	5.0	10	1	1.4	1	0	4.8	P	3.2	P	n	?
19	142.5	47.0	Nov	15.8	6	0	1.6	2	0	2.3	MA	2.5	MA	n	?

Figure 2. External appearance of the ovaries from immature females aged 0 (a) and 5 years old (b), and from mature females aged 7 (c) and 17 years old (d), to the same scale (in mm). A large corpus albicans protrudes from the left ovary in (c). The top half of the left ovary in (d) consists of a large, round corpus luteum. Several medium corpora albicantia show as wrinkly surface scars on the bottom half of this same ovary (d).


90
100
110
120
a
b
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d

had recently aborted her fetus about halfway through the pregnancy (see section on pathologies below).

The pregnant female died late December with an approximately 4-5 week old embryo. Small cetaceans generally have gestation periods between 10-12 months (Perrin and Reilly 1984). Data from the pregnant and recently aborted female, and field data showing that calves are born during the months of November to February (Slooten and Dawson 1988), are consistent with this general pattern.

Accumulation of corpora albicantia: Onset and rate of ovulation

The ovaries of all females that were at least 7 years old contained one or more CA. Three females, 7, 9 and 10 years old, each had a single CA. The other four mature females, 9, 14, 17 and 19 years old, each had more than one CA of a range of sizes (Table 2). The 7-year-old female had the largest single CA in the sample. This large CA was still cellular, with collagen replacement of the luteal cells just beginning, and with prominent and apparently healthy bloodvessels. The single CAs found in the ovaries of the other two females showed progressively more replacement of old CL tissue with collagen, coincident with the reduction in CA size. The size and histology of these single CAs, as well as the date of death and uterus histology (see below), indicate that one female gave birth to her first calf at age 7, and the other two females gave birth at age 8 or 9. These data indicate that female Hector's dolphins give birth to their first calf at an average age of approximately 8 years, with an average age at first ovulation 1 year prior, at 7 years of age.

Table 2. Number and size distribution of corpora albicantia per female.

Age	Corpora albicantia			
(yrs)	Total	Small	Medium	Large
7	1	0	0	1
9	1	0	0	1
9	6	0	6	0
10	1	0	0	1
14	4	1	2	1
17	11	3	8	0
19	8	6	2	0

The three females with one CA, and two females with one CL suggest that ovulations generally occur one at a time. In addition, none of the females had more than one large CA in their ovaries (Table 2), suggesting that by the time the next CA appears, the previous one has decreased in size to the medium CA stage. The sample size is too small to determine whether CAs persist for the lifetime of the female, but their accumulation with age is consistent with this hypothesis. Certainly the overall increase in CA count with age shows that a CA persists at least until the next ovulation, and presence or absence of CAs and CLs is therefore a reliable indicator of sexual maturity. This is supported by the lack of serosal stretch marks on the uteri of females without CAs in the ovaries, and their presence in the females with CAs. Assuming that CAs persist, and based on an average age at first ovulation of 7 years, ovulation rates of 0.5, 0.62, 0.92 and 2.3 per year were calculated for the four females with more than one ovulation scar.

The uterus and age at first reproduction

To help determine the age at which females give birth to their first calf, uterus samples of the mature females were examined histologically in an attempt to correlate ovarian status with endometrial changes.

The three females with one CA in their ovaries showed a range of endometrial stages. The uterus showing signs of the most recent pregnancy belonged to the 7-year-old female, with the largest single CA. The endometrium contained sparse glands without secretion or mitoses and a prominent blood supply following a recent parturition, and can be described as "mature-lactating" (Lockyer and Smellie 1985). Field data indicate that calves are born during the spring/summer months of November to February (Slooten and Dawson 1988). This dolphin was killed in a gillnet in late January, and probably gave birth up to two and a half months before death.

The endometrium of the 9-year-old female with one CA was in the mature-anoestrus stage (Lockyer and Smellie 1985), with undeveloped glands and a less prominent blood supply than seen in the 7-year-old female. This female's uterus histology, and the smaller size of her CA, indicate she gave birth less recently than the 7-year-old. The 9-year-old female was killed in a trawl-net in

December and could have given birth earlier that season, or during the previous season at 8 years of age.

The endometrium of the third female with one CA was undergoing early stimulation of the follicular or proliferative phase (Finn and Porter 1975), with glands more numerous and coiled, and occasional secretory vacuoles. The endometrium was slightly more developed than the mature-anoestrus stage, but certainly not mature-ovulating (Lockyer and Smellie 1985). This 10-year-old female was drowned in a gillnet in October. All indications are that she gave birth the previous year, or the year before that, at 8 or 9 years of age.

Two of the mature females with more than one CA in their ovaries had endometria in the mature-anoestrus phase. The uterus lining of the pregnant female was typically thick and blood-engorged. The inner surface of the endometrium had a relatively smooth appearance, with only a few crypts forming, contrasting with the dendritic appearance expected in later stages of pregnancy (Lockyer and Smellie 1985). The remaining mature female had recently aborted (see below). The endometrium of her uterus was thick and blood-engorged, confirming a very recent pregnancy. The inner surface of the endometrium was strongly dendritic, as would be expected in mid or late pregnancy.

Atresia and corpora atretica

Atresia is the process of degeneration that affects the majority of follicles in all mammals (Peters and McNatty 1980). Of a pool of growing follicles only one (or a small number) ovulates in each development cycle, and the rest degenerate. Follicles may become atretic at any stage of their development (Peters and McNatty 1980), and give rise to secondary interstitial tissue, small, inconspicuous fibrous scars, or accessory CLs (Perrin and Donovan 1984). Follicles at a range of stages of development and atresia were present in the Hector's dolphin ovaries examined, but no accessory CLs were noted.

Corpora atretica may result from follicles which have ovulated without adequate luteinization, or luteinized without ovulation, respectively (Perrin and Donovan 1984; Marsh and Kasuya 1984; Best 1967), and it is possible to confuse these with CAs. All the fibrous bodies found in the Hector's dolphin ovaries examined here fitted into the "normal" pattern of development and atresia (see Perrin and Donovan 1984). I found no evidence to suggest that

any of the small CAs had resulted from luteinization and atresia of follicles which had not ovulated. The stigma appears to become progressively less obvious as a CA ages, and, in this sample, there appear to be no histogical criteria on which to distinguish small corpora of approximately the same size with and without an obvious stigma.

Pathologies

Few cases of pathology of reproductive tracts in cetaceans have been reported (Perrin and Donovan 1984; Benirschke and Marsh 1984; Lockyer 1984). In this study two cases of pathology were found. One female had a follicular cyst in each ovary, and another female had recently aborted a fetus.

The follicular cysts were found in the ovaries of the oldest female (19 years old). Each cyst was shaped like a fluid-filled balloon with thin walls, and they measured 43 x 33 x 18mm and 10.5 x 9.6 x 9mm, respectively, with the largest cyst in the left ovary. Histology of the walls of the cysts showed a prominent layer of thecal cells, and a very thin layer of granulosa cells which in many places was detached from the theca interna and in places was missing altogether.

One of the two females with a CL appeared to have recently aborted a fetus. The uterus was stretched and enlarged (see Table 1 and Fig. 1d), and the histology of the endometrium confirmed a very recent pregnancy. This 9-year-old female died in June, some four months before the time of year when the earliest newborn calves are seen in the field. The most likely interpretation of the histology of the ovaries and uterus is that this female aborted an approximately half-term fetus some days before she died. She was found dead on a beach, and the first person on the scene reported blood oozing from the genital-anal area.

Discussion

Age at first reproduction and length of reproductive period

Females 5 years old and younger had immature ovaries and uteri. Three females, 7, 9 and 10 years old, had just had their first ovulation, which in each case had been a single ovulation and had resulted in pregnancy. Age at first reproduction was estimated at 7 years of age for one of these females and 8 or 9 for the other two, and the oldest female was 19 years old (Chapter 1). The

increase in CA count with age shows that each CA persists at least until the next ovulation, and presence or absence of CAs and CLs is therefore a reliable indicator of sexual maturity. This was confirmed by the presence of serosal stretch marks on the uteri of the females with CAs, and their absence in those females without CAs.

It is possible that the minimum age at first reproduction in the population is one year lower than shown in this study. The large number of young females in the sample clearly show that females 4 years old and younger have not yet ovulated. It is therefore most unlikely that any females have their first calf at age 5. However, it is possible that some females have their first ovulation at age 5 and their first calf at age 6. This sample included one 5 year old female, who had not yet ovulated, and no 6-year-olds. All available data indicate a minimum age at first reproduction of 7 years old. However, it would be useful to examine a larger sample of females between 5 and 9 years old.

Commerson's dolphin, *C. commersonii*, is the only other species in the *Cephalorhynchus* genus for which sufficient reproductive data are available for comparison. Lockyer et al. (1981, 1988) examined tooth sections of 136 Commerson's dolphins found on beaches in Tierra del Fuego. The maximum age in this sample, which consisted of a wide range of ages and sizes, was 18 years old. Collet and Robineau (1988) and Lockyer et al. (1981, 1988) have studied reproductive material from Commerson's dolphins collected at the Kerguelen Islands and Tierra del Fuego respectively. The Kerguelen Islands sample included seven females (aged 4 [two individuals], 5, 6, 7, 9 and 10 years), and Collet and Robineau (1988) found that the ovaries of all individuals that were at least 5 years old contained CAs and CLs. The Tierra del Fuego sample included ovaries of eight females (0, 3, 4 [two individuals], 8 [two individuals], 10 and 18 years old), and the results suggested that females of 4 years and younger were immature, while those 8 years and over were mature or maturing (Lockyer et al. 1981, 1988).

The larger sample size available for *C. hectori*, 32 females compared with a total of 15 females for *C. commersonii*, allows greater accuracy in the estimate of age at first ovulation and age at first reproduction. Furthermore, the large number of younger, immature females in the sample, increases confidence that the estimate of age at first reproduction is representative.

Hector's dolphins may reproduce less often as they get older. It is usual for reproductive pathologies to be more common in older females (Labhsetwar 1970), and in this study it was the oldest female who had the follicular cysts. There was also evidence of the usual coincident drop in fertility (Bartlett et. al. 1986), as the female with the cysts showed no signs of recent ovulation, whereas all other mature females had either a CL or a large CA in their ovaries. There is evidence for a reduction in fertility in older females of several species of cetaceans, and a definite post-reproductive, menopausal phase has been demonstrated for pilot whales *Globicephala macrorhynchus* (Marsh and Kasuya 1984).

Ovulation rate

Ovulation rate is a vital parameter in many population models for cetaceans (Perrin and Donovan 1984), and it is generally assumed that CAs persist for the lifetime of the female and can be used to estimate ovulation rate. Work is continuing to determine whether this is a reasonable assumption (e.g. Perrin and Donovan 1984). If old CAs disappeared from the ovary, one would expect their size distribution to be negatively skewed and the modal value to decrease with age (Marsh and Kasuya 1984). Marsh and Kasuya showed that neither of these expectations were fulfilled in pilot whales, and presented strong evidence that CAs persist for life in that species.

Unfortunately the sample size here is too small to use these techniques to determine whether CAs persist for the lifespan of female Hector's dolphins, but their accumulation rate with age suggests that they are likely to do so. The numbers of CAs for the older females suggest that the ovulation rate is variable between females, as one would expect, and that for each female the total number of CAs increases with age.

The three females with one CA and two females with one CL suggest that ovulations are generally single. Based on an average age at first ovulation of 7 years, the four females with more than one CA had ovulation rates of 0.5, 0.67, 0.92 and 2.3 ovulations per year, respectively. The two lowest ovulation rates are consistent with a single ovulation per year and field observations of females having one calf every 2 to 3 years. The two highest ovulation rates, however, suggest multiple ovulations do occur. The highest ovulation rate of 2.3 per year came from a female who had accumulated 6 CAs and 1 CL by the time she was 9 years old. Age at first ovulation is likely to vary from female to

female, but at an ovulation rate of one per year this female would have had to start at age 2 or 3, at which age all females in the sample had undeveloped ovaries and uteri. The 6 CAs in this female's ovaries were all medium CAs of a similar size (Table 2), suggesting that they were the result of a multiple ovulation. In contrast, the other females had CAs of a range of sizes. The most likely explanation is that this female had a multiple ovulation when 7 or 8 years old, followed by a single ovulation and pregnancy at age 9. It seems likely that the female with an ovulation rate of 0.92 per year had ovulated more than once in some years and not at all in others. Of course, a calculated ovulation rate for a given female, based on average age at first maturity, will still be in error to the extent that the age at first maturity varies from female to female.

Collet and Robineau (1988) suggested that the ages and number of CAs of female *Cephalorhynchus commersonii* in their sample indicated an ovulation rate of 0.5 to 1.2 per year. However, they pointed out the alternative approach of using the number of CAs to calculate age at first ovulation, assuming a constant ovulation rate of one per year. Collet and Robineau (1988) cautioned that ovulation rate and age at sexual maturity were likely to vary from female to female, and that their small sample precluded any firm conclusions on age at sexual maturity or ovulation rate.

Evidence for multiple ovulations has been recorded for *C. commersonii* from two studies. Lockyer et al.'s (1988) sample of eight female *C. commersonii* included an 8-year-old female with one CL and 11 CAs. In this female, 10 of the CAs were at a similar stage of regression, and Lockyer et al. concluded that multiple ovulation had probably taken place. Similarly, Collet and Robineau's (1988) study of seven female *C. commersonii* included one 9-year-old female with one CL and five CAs, which could indicate multiple ovulation. Adding Collet and Robineau's and Lockyer et al.'s findings, two in six mature female *C. commersonii* showed evidence of an ovulation rate greater than one per year. The data reported here for *C. hectori* suggest an incidence of one or two in seven. In both species multiple ovulations appeared more likely just following sexual maturity.

Gaskin et al. (1984) found that female harbour porpoises *Phocoena phocoena* reach sexual maturity at 4 to 6 years old, but counted up to 15 CAs in some females only 4 and 5 years old. They concluded that younger females, which

are not yet fully incorporated into the breeding population, regularly have multiple ovulations without fertilization.

These observations emphasize the importance of determining age at first reproduction as separate from age at first ovulation. Fortunately, direct information on age at first reproduction is available in this study, as the three females with one CA had all been pregnant.

Reproductive rate

The reproductive rate discussed here is the gross reproductive rate or birth rate, which does not take into account deaths in the population. Estimates of net reproductive rate are discussed in Chapter 4. The ovulation rate provides important insights into reproductive rate, and sets its upper limit, but the number of CAs in the ovaries of a female can not be equated directly with the number of times that female has been pregnant. Studies of the histology of cetacean CAs and CLs which have resulted from fertilized and unfertilized ovulations are continuing, but the consensus view is that it is not possible with currently available techniques to distinguish between them (Perrin and Donovan 1984). No histological differences were noted in the Hector's dolphin material. If such differences are found in future, the ovaries contain a count of the number of pregnancies as well as the number of ovulations.

Studies of reproductive tissues with accompanying age estimates can provide an estimate of age at first reproduction. However, field observations on free-living dolphins are necessary to provide estimates of the number of births per female per year after that age has been reached. Minimum calving intervals for dolphins range from 2 to 4 years (Perrin and Reilly, 1984; Reilly and Barlow, 1986). Field data on photographically identified individuals indicate that Hector's dolphins fall within this range, reproducing every 2 to 3 years (Slooten and Dawson In press). The data on lactation and pregnancy support this, as neither of the two pregnant females were lactating and neither of the two lactating females were pregnant.

This reproductive output is similar to that of other small cetaceans such as the harbour porpoise *Phocoena phocoena*, and the franciscana dolphin *Pontoporia blainvillei*. The harbour porpoise, with an average length of 1.4m, becomes sexually mature between 4 and 6 years of age, lives to a maximum age of about 12-13 years and has a calving interval varying from 1 to 3 years

(Gaskin et al. 1984). On the basis of these reproductive parameters, Gaskin et al. (1984, p.145) concluded that this species may have "a short lifespan, with no more than about three or four calves produced on average by each mature female". Similarly, a 2-year breeding cycle has been reported for *P. blainvillei* (Brownell 1984; Kasuya and Brownell 1979). Many of the larger odontocetes also have very low reproductive rates. Female short-finned pilot whales *Globicephala macrorhynchus* mature at 7-12 years old, live to a maximum of 63 years, but have their last calf before age 40 and produce only about four or five calves per lifetime (Kasuya and Marsh 1984).

Apparently, captive Commerson's dolphins *C. commersonii* at Sea World in San Diego also breed once every 2 years at most (Sea World staff, pers. comm.). The exception to this rule was a female who conceived again during the same season after losing a calf, resulting in births in two subsequent years. No long-term photo-identification studies have yet been conducted to determine calving intervals of this species in the wild.

With an average age at first reproduction of 7-9 years, a maximum age of around 19 years and a calving interval of 2-3 years, a female Hector's dolphin could produce a maximum of four to seven calves in her lifetime.

Chapter 3
Changes in the male reproductive organs of Hector's dolphins with age and reproductive activity

Abstract

Reproductive tracts of male Hector's dolphins were recovered from individuals found dead on beaches, or accidentally killed in gillnets or trawlnets. Macroscopic and histological examination indicated that males reach sexual maturity when they are between 6 and 9 years old. Insufficient data were available to test for the presence or absence of a seasonal cycle of spermatogenesis. However, both testis weights and sperm numbers appeared to peak in December (early austral summer). Hector's dolphins have extraordinarily large testes relative to their body size. The maximum found in this study was a 41.5kg male with testes (including epididymides) totalling 1.21kg. This is consistent with behavioural data suggesting that Hector's dolphins have a polygynous or promiscuous mating system with frequent copulations.

Introduction

Rational conservation management is impossible without information on the reproductive biology of the species involved. Besides being required for the calculation of population growth rates, data on male and female reproductive function provide insights into the mating system of the species which may be important in interpreting the conservation implications of population modelling work. Hector's dolphin *Cephalorhynchus hectori* has been subject to an alarming level of incidental entanglement in gillnets (Dawson 1990). The reproductive biology of female Hector's dolphins is discussed in Chapter 2, and this chapter presents data on male reproductive biology.

The question of what constitutes sexual maturity is more complex for males than for females, for two main reasons. Firstly, males which are actively producing sperm are not necessarily behaviourally mature and participating in mating behaviour. Secondly, in several dolphin species males appear to go through a seasonal cycle of testicular activity, and during the resting phase there may be a reduction in testis size and an absence of sperm in the epididymis (Perrin and Reilly 1984; Collet and Saint Girons 1984). The first

problem is virtually impossible to solve. Dolphins often engage in non-reproductive sexual behaviour, sometimes including obviously immature individuals (McBride and Kritzler 1951), making it very difficult to study the relationship between sperm production and social maturity in a population under natural conditions. The second problem can be alleviated if the relative abundance of other reproductive cells besides spermatozoa is taken into account.

Methods

Sixty dead Hector's dolphins were available for examination (Slooten and Dawson 1988, and In press), and age estimates were available from tooth sections (Chapter 1). Of the 27 males, seven had been dead for several days. Reproductive samples of the remaining 20 were examined histologically. Testes (including epididymis) were weighed, measured and photographed, and then stored in 10% formalin. Samples taken from the centre of the testis and epididymis were embedded in paraffin wax, sectioned at approximately 5μ and stained with haematoxylin and eosin. The samples were taken from the centre, as there is evidence that this part of the testis matures earlier than the periphery (Best 1969).

Males were defined as immature, pubertal, mature or resting according to the following criteria, adapted from Collet and Saint Girons (1984), Hohn et al. (1985):

Immature. The seminiferous tubules are narrow (approx. 40-60μ in diameter) and embedded in abundant interstitial tissue. Spermatogonia, but no other stages of germinal cells are observed. The epididymis has a completely empty lumen.

Pubertal. The interstitial tissue occupies very little space between the seminiferous tubules which have lengthened but are still relatively narrow. Spermatogonia and spermatocytes are present. Occasional spermatids are found, but no spermatozoa.

Active-mature. Almost no interstitial tissue is present. Relatively few spermatogonia and spermatocytes, but many spermatids and spermatozoa are seen. The lumen of the epididymis is often full of spermatozoa.

Resting-mature. The testes are of a similar size and appearance to those of active mature males, but there are almost no spermatozoa, very few

spermatids, and a medium density of spermatogonia and spermatocytes. The epididymis epithelium has a resting appearance, and the lumen contains only very few spermatozoa and a few spermatids.

Results

Reproductive morphology is essentially as described by Collet and Robineau (1988) for *Cephalorhynchus commersonii*. The testes of Hector's dolphins, as of the other species in the genus *Cephalorhynchus*, are very large in relation to their body size. The maximum found here was a 41.5kg male with testes (including epididymides) totalling 1210g (Table 1).

The histology showed one male to be pubertal (as defined above), and all the others to be immature or active-mature (Table 1). Testis weight as well as stage of maturity increased with age and body length (Table 1). Males up to 3 years old had small, immature testes with summed testis weights of less than 30 grams. Those 9 years old and older all had mature testes with summed testis weights ranging from 304 to 1210g. One of the 4-year-old males had a summed testis weight of 53g, and was immature, while the 6-year-old, with summed testis weight of 65g was pubertal. Thus sexual maturity in male Hector's dolphins appears to be attained somewhere between 6 and 9 years of age.

Seasonal variation in testis weight of mature males suggests a peak of spermatogenesis and sexual activity in early to mid summer. The highest testis weights were recorded in December, with lower testis weights in January and February. Relatively large numbers of spermatids put all mature males in the "active mature" category, but the variation in the number of spermatozoa present followed a similar trend to the testis weights. A larger sample size and more samples outside the summer months are needed before any firm conclusions can be drawn about the presence or absence of seasonal cycles in spermatogenesis.

Discussion

Sexual maturity in male Hector's dolphins appears to be reached between 6 and 9 years old, at a similar age to the females. This is within the range expected for male delphinids of this size range (Perrin and Reilly 1984).

Table 1. Age, weights, measurements and stage of maturity of Hector's dolphin males. Testis weights include the epididymis. Stages of maturity (determined histologically): AM = active-mature; I = immature; P = pubertal.

Age (yrs)	TL (m)	Body weight (kg)	Month of death	Testis weights (g) Left	Right	Total	Stage of maturity
0	96.0		Dec				
1	109.0	26.4	Jan	8	7	15	I
1	104.6	21.9	Jan	8	7	15	I
1	107.5	26.5	May	8	7	15	I
1	119.0	20.4	Sep				
2	119.2	20.4	Jan	9	10	19	I
2	111.0	25.6	Feb	8	7	15	I
2	113.0	25.7	Feb	12	11	23	I
2	114.0	28.5	Feb	11	13	24	I
2	113.5	28.4	Nov	8	9	17	I
2	117.0	31.0	Dec	9	9	18	I
2	119.0	33.0		10	14	24	
3	119.0	27.0		8	9	17	
3	122.0						
4	118.8	24.5	Apr	11	10	21	I
4				25	28	53	I
6	119.0	30.8	Nov	32	33	65	P
9	127.0	41.5	Dec	492	522	1014	AM
9	129.0	36.0	Dec	383	390	773	AM
11	118.5	33.5	Dec	348	356	704	AM
11	132.0	37.6	Feb	164	140	304	AM
13	127.0	28.0	Jan				
15	130.0		Jan	215	210	425	AM
16	119.5		Jan	234	230	464	AM
18	125.0	41.5	Dec	616	594	1210	AM
18			Jan				
20	117.0	31.0	Dec	366	416	782	AM

Estimates of age at attainment of male sexual maturity are in the range of 6 years for *Delphinus delphis* (Collet and Saint Girons 1984), 8-9 years for *Stenella coeruleoalba* (Kasuya 1976; Miyazaki 1977), and 8.5-11.5 years for *Stenella longirostris* (Perrin et al. 1977). Males of the larger delphinids tend to mature later, at approximately 12 years for *Tursiops truncatus* (Sergeant et al. 1973) and about 8-14 years for *Pseudorca crassidens* (Purves and Pilleri 1978).

Within the genus *Cephalorhynchus*, information on sexual maturity is available for *C. commersonii*. Collet and Robineau's work on *C. commersonii* from the Kerguelen Islands suggests an age at first maturity for males between 7 and 9 years old. Their sample of male dolphins consisted of two immature individuals aged 4 and 5, a pubertal male aged 7 and a mature male aged 9. Lockyer et al. (1988) noted a marked increase in testis weight between 5 and 6 years in *C. commersonii* from South American waters (n=19), and found sperm in the testes of three of the 10 individuals who were 6 years old and older.

Many adult cetaceans show a seasonal increase in the size and spermatogenic activity of the testis, coincident with the period of conception (Perrin and Reilly 1984; Lockyer 1984). Too few data are available to test this theory for Hector's dolphin or the other three *Cephalorhynchus* species. However, an apparent peak in spermatogenesis during mid to late summer suggests that this may be the case for Hector's dolphins. Births take place during early to mid summer, and the gestation period is most likely between 10 and 12 months (Chapter 2).

Hector's dolphins are unusual among mammals in that males are smaller than females (Chapter 1) and have proportionately very large testes. Dolphins and porpoises are renowned for having large testes relative to body mass (Kenagy and Trombulak 1986), and Hector's dolphins are at the large end of the range even compared with other dolphins and porpoises. The highest ratio of testis to body weight for Hector's dolphins in this study (2.9%) was surpassed only by some rodents and the harbour porpoise *Phocoena phocoena* in Kenagy and Trombulak's (1986) sample.

Both intra and inter-specific variation in relative testis size is thought to reflect the amount of sperm used and the frequency of copulations (Setchell 1978;

Kenagy and Trombulak 1986). To improve his chances of fertilizing females, a male can either copulate with as many females as possible, or stay with a female or group of females he has copulated with and try to prevent other males from copulating with them. Brownell and Ralls (1986) discussed mating systems in baleen whales and suggested that mate monopolization is likely to be more common in species with relatively small testes. They argued that in baleen whale species with relatively small testes, males may compete primarily by monopolizing females and preventing other males from copulating with them. In these species females are thought to copulate with one or a small number of males each season, and male-male interactions are often highly aggressive. Better behavioural data are available on mating systems in baleen whales with relatively large testes (e.g. right whales), which Brownell and Ralls (1986) suggested would tend to have promiscuous mating systems in which male-male interactions are not highly aggressive.

The relatively small body size of male Hector's dolphins suggests that aggressive male-male competition and monopolization of females are not important features of their mating system. Ralls (1976) reviewed mammals in which females are larger than males and concluded that the phenomenon is not correlated with polyandrous mating systems. She suggested that large females are more likely in species in which the lack of some resource is more critical to the reproductive success of females than of males (Ralls 1976). In cetaceans, as in primates (Leutenegger and Cheverud 1985; Cheverud et al. 1985), the distribution of body size dimorphism among taxa suggests that scaling and phylogeny have a strong influence. Females are larger than males in all ten species of baleen whales, despite a wide range of testis sizes and apparent mating systems in this group (Brownell and Ralls 1986). In the toothed whales, females are larger in the smallest species including Commerson's dolphin (Goodall et al. 1988a), harbour porpoise (Gaskin et al. 1984) and the river dolphins (Brownell 1984).

Whatever the evolutionary causes, the combination of relatively large testis size and relatively small males suggests that Hector's dolphins have a promiscuous mating system with frequent copulations and relatively little aggression between males. Field data are consistent with this hypothesis. Overt aggression is rare, and the number of sexual behaviours per individual is highest in relatively large groups and tends to increase after groups come together (Chapter 7). Association patterns between individual Hector's

dolphins are relatively fluid (Chapter 6), as in other dolphin species such as bottlenose dolphins (Wells 1986; Wells et al. 1987). Wells et al. suggested that the bottlenose dolphins they studied in Florida had a promiscuous mating system, with males increasing their reproductive opportunities by moving between female groups rather than monopolizing access to any given female(s).

Recent research on sperm whales *(Physeter macrocephalus)* has highlighted the management and conservation implications of such a social system (Whitehead 1987). Male sperm whales move from one group of females to another, searching for sexually active females rather than defending a "harem" as was previously thought (Whitehead 1987; Whitehead and Arnbom 1987). This means that the fertilization rate of the population depends in part on the amount of time needed for a male to travel between groups relative to the length of time each female is fertile and the degree of synchrony between females (Whitehead 1987). It is difficult to predict the specific consequences of a population decrease for pregnancy rates in Hector's dolphins. However, if males search for rather than monopolize females, there are more likely to be times when a fertile female is not accompanied by a mature male and not fertilized. Such a mating system is likely to result in relatively high fertilization rates in areas where Hector's dolphins are common, but could depress fertilization rates in low density areas.

If population densities changed such that males stood a much better chance of finding sexually active females by staying with a group than by travelling around, one might expect males to alter their mate searching behaviour. Patterns of mate searching in mammals and birds are relatively flexible, and may change with environmental conditions (Rubenstein and Wrangham 1986). However, there are several reasons why changes in mate searching behaviour may not improve or maintain the population fertilization rate. Firstly, the travel time may remain acceptable to males long past the point where female reproductive rates have started to decline. Secondly, the distribution patterns of both sexes are not determined solely by reproductive needs, but also by the distributions of food and predators (Rubenstein and Wrangham 1986). Food availability may force a species into distribution patterns which depress pregnancy rates. Thirdly, searching for sexually active females by moving around may be the only option open to male Hector's dolphins. They may never change to a polygynous or monogamous mating system if the

smaller males are incapable of preventing individual females, let alone groups, from mating with other males.

The very small and localized population of Hector's dolphins, 3000-4000 individuals and found only in New Zealand waters, makes them vulnerable to pollution and incidental kills in fishing operations. The large number of deaths in gillnets (Dawson 1990) has undoubtedly had a major impact on the population, and the decrease in numbers may have increased the distance males have to travel to find sexually active females. Comparative studies of calving rates in areas of high and low dolphin density are needed to help determine if this is a problem for Hector's dolphin.

Of more immediate concern is the unfortunate coincidence of Hector's dolphin calving and mating activity with the time of year when human interference is greatest. Commercial and amateur fishing activity as well as recreational boating increase dramatically during summer. Unfortunately, this is the time of year when Hector's dolphins move closer inshore, have their calves and appear to do most of their mating. For these reasons, protective measures such as gillnetting restrictions need to be strongest in summer.

Chapter 4
Population biology and conservation of Hector's dolphin

Abstract

During the past decade, Hector's dolphins *Cephalorhynchus hectori* have suffered an alarming level of entanglement mortality in commercial and amateur gillnets. Here we study two Leslie matrix population models that incorporate known features of dolphin fertility and mortality, focussing on the information they provide regarding age distributions and maximum population growth rates. The simplest model specifies constant survival rates over many age-classes. The second model uses more realistic curves of age-specific survival rates. The results indicate that Hector's dolphin, like most other small cetaceans, has a low potential for population growth. Growth rates of 1.8 to 4.4% per year are likely to be the maximum possible for Hector's dolphin populations, and *C. hectori* (and *C. commersonii)* populations are likely to be declining under recent levels of net entanglement. Survival rate estimates from free-living populations, subject to natural and net-entanglement mortality, resulted in decreasing populations. Even with the most optimistic reproductive parameters, survival rates would need to be some 5 to 10% higher than those observed in populations subject to gillnet entanglement, before population growth could occur. The likely consequences of a reduction in entanglement mortality through conservation management are explored using the survivorship curve model. These simulations show that the age structure of the population can have an important effect on changes in the size and growth rate of the population during the recovery phase following a reduction in entanglement mortality.

Introduction

Cephalorhynchus is a genus of four small dolphin species, each restricted to a relatively small area of inshore coastal habitat in the Southern Hemisphere. Hector's dolphin *Cephalorhynchus hectori* is the smallest of the four and the smallest oceanic dolphin, sexually mature adults usually being 117-145cm in total length (Slooten and Dawson 1988). This species is found only in New Zealand waters, and is most abundant along the east and west coasts of the South Island. A boat survey of the distribution and abundance of Hector's

dolphin indicated a total population of 3000-4000 individuals (Dawson and Slooten 1988).

All four *Cephalorhynchus* species are caught incidentally in gillnetting operations, and *Cephalorhynchus commersonii* and *C. eutropia* are also caught intentionally for use as crab bait (Goodall and Cameron 1980; Perrin 1987). Hector's dolphins are not subject to a directed catch, but are regularly entangled in commercial and amateur gillnets. The precise level of this incidental catch is unknown, and has varied over time and between areas. It appears to be particularly severe around Banks Peninsula (43° 50'S, 172° 56'E), in both Pegasus Bay to the north and Canterbury Bight to the south (Dawson 1990). In this area, where a relatively high density of Hector's dolphins coincides with intensive inshore gillnetting, entanglement rates have probably been high since the mid-1970's (Cawthorn 1988; Dawson 1990). Between 1984 and 1988, the total number of Hector's dolphin entanglements reported by fishers in the Pegasus Bay-Canterbury Bight area exceeded 30% of the estimated 1984/85 population, and the entanglement rate exceeded 10% of the population in one of the four years for which entanglement was monitored (Dawson 1990).

Due to its limited range, small population size, and susceptibility to gillnet entanglement, *C. hectori* is vulnerable to local depletion and possibly extinction. The IUCN Red Data Book currently lists *C. hectori* among the "threatened" species of cetaceans. Until recently, the development of effective conservation and management programmes for Hector's dolphin has been impeded by a paucity of information on its population biology.

In this paper we report a range of possible population growth rates and age distributions for Hector's dolphin, using simple population models based on what is known or can be inferred about their age-specific survival and fertility rates. The simpler model specifies constant survival rates over many age-classes, following the methods of Reilly and Barlow (1986) and providing a comparison with their results on the natural rate of increase for other dolphin species. In a second and more realistic model, survival rates are represented as varying throughout the lifespan using a set of survival rate curves similar to those found in other mammals (Barlow and Boveng In press). This model provides an improved understanding of age distribution phenomena for Hector's dolphin. The second model, and the computational method

presented here, are particularly useful for exploring the fluctuations which may be expected in a population after survivorship is improved through conservation management.

The results of these population models formed part of the background data which led to the formation of a Marine Mammal Sanctuary around Banks Peninsula in November 1988 to reduce gillnet entanglement in this area. The likely effects of this change in conservation policy are explored using the survivorship curve model. The Hector's dolphin population in the Pegasus Bay-Canterbury Bight area is likely to have suffered high entanglement rates for at least the last 15 years, as the area has been subject to intense gillnetting effort during those years (Dawson 1990). Two simulations explore what would happen to the population if an entanglement rate of 10% per year were reduced to 5%, or to zero.

Methods

In section 1 we formulate the mathematical structure of our computations, and in section 2 we discuss the specific values of fertility and survival rates for Hector's dolphins.

1. Two population models based on the Leslie Matrix

Population growth rates for Hector's dolphin were calculated using a Leslie matrix model (Leslie 1945), a simple projection model in which only females are considered. Assuming that age-specific rates of mortality and fertility remain constant over time, the Leslie matrix model projects the expected population age distribution for time t+1 by means of the matrix equation:

[1] $$N_{t+1} = M \cdot N_t$$

where: $$N_t = \begin{bmatrix} N_{1\,t} \\ N_{2\,t} \\ N_{3\,t} \\ N_{4\,t} \\ . \\ . \\ . \\ N_{L\,t} \end{bmatrix}$$

$N_{j\,t}$ is defined as the number of dolphins alive aged j at time t, and the letter L denotes the maximum lifespan of the species. The matrix M, called the "transition matrix" contains the fertility and survival rates, denoted by f_x and s_x respectively, where $f_x \geq 0$, and s_x ranges from 0 to 1:

$$M = \begin{bmatrix} f_1 & f_2 & f_3 & f_4 & \dots & f_{L-1} & f_L \\ s_1 & 0 & 0 & 0 & \dots & 0 & 0 \\ 0 & s_2 & 0 & 0 & \dots & 0 & 0 \\ 0 & 0 & s_3 & 0 & \dots & 0 & 0 \\ 0 & 0 & 0 & s_4 & \dots & 0 & 0 \\ . & . & . & . & & . & . \\ . & . & . & . & & . & . \\ . & . & . & . & & . & . \\ 0 & 0 & 0 & 0 & & s_{L-1} & 0 \end{bmatrix}$$

Each column contains the f_x and s_x value for one age-class of dolphins (1 year), and the number of columns in the matrix corresponds to the longevity of the species. The survival rates s_x are simply the probability that an individual of age group x will survive to enter age group x+1. The fertility rates f_x represent the expected proportion of females aged x who produce a female offspring during that year. Except in very rare cases, dolphins give birth to one calf at a time (Perrin and Reilly 1984).

The usual rule for Leslie matrix models is that offspring are born at the beginning of the model "year", and must survive to the end of the year to enter age-class 1. In our model, which follows the methods of Reilly and Barlow (1986) and Barlow (1986), calves are born just before the end of the year, i.e. the years in our model begin immediately after the calving season. Thus, the first age-class corresponds to newborn calves, and the fertility rate is specified as the number of female offspring born per year per female aged x, multiplied by the adult survival rate. Thus, the fertility rate is calculated using the adult survival rate (the probability that the mother will survive to the calving season to give birth), rather than the calf survival rate.

Leslie (1945) showed that if fertility and survival rates remain constant over time, the expected age structure and total population size at any future time

can be found by premultiplying the column vector of the present age structure N_t by the transition matrix M an appropriate number of times:

[2] $$N_{t+k} = M^k N_t.$$

An important feature of such "population projection" modelling is that each matrix of f_x and s_x values generates an associated stable age structure and equilibrium population growth rate. If the f_x or s_x values change, for example due to a reduction in food abundance or a change in conservation policy, the age structure and growth rate of the population are expected to converge, after a period of fluctuation, to the different values associated with the new survival and fertility rates. The speed of this convergence depends on the magnitude of the changes in the survival and fertility rates. Once a stable age structure has been reached, the expected population size increases exponentially at the new equilibrium growth rate, or decreases exponentially if the equilibrium growth rate is negative. The stable age structure and the equilibrium growth rate depend on the values of f_x and s_x that constitute the transition matrix M, and are independent of the initial age distribution.

As an alternative to the Fortran computer program used by Reilly and Barlow (1986), Slooten developed a computational technique using a "spreadsheet" program on an Apple Macintosh SE computer. In Reilly and Barlow's program, the equilibrium growth rate of the population is calculated from the largest eigenvalue of the transition matrix of fertility and survival rates (M). In contrast, the spreadsheet calculates the growth rate iteratively, by repeatedly multiplying N_t with M. Thus, not only the resulting equilibrium growth rate is calculated, but it is also possible to examine the fluctuations in population size and population growth rate after a change in fertility or survival rates.

1.1 The Reilly-Barlow model

Our first model is based on the methods of Barlow (1986) and Reilly and Barlow (1986) in their models of porpoise and dolphin populations. They chose to keep fertility and survival rates constant over many age-classes, because of data limitations for dolphins and porpoises. Both Barlow (1986) and Reilly and Barlow (1986) used the calf survival rate for the first year of life only, and a constant adult, or non-calf survival rate for all age-classes thereafter. The choice of a separate survival rate for calves was based on the common observation of higher mortality in juvenile mammals (e.g. Caughley

1977). Reilly and Barlow recognized that juvenile mortality factors probably extend past the first year of life, but felt that there were insufficient data for dolphins to justify including this in their model.

1.2 The survivorship curve model

The typical mortality pattern for mammals consists of an initial period of high mortality, followed by a period of relatively low mortality, and concluding with a period of rapidly increasing senescent mortality (Caughley 1977; Siler 1979). We calculated age-specific survival curves for Hector's dolphin following Barlow and Boveng's (In press) approach, which, in turn was based on Siler's (1979) model. In Barlow and Boveng's (In press) model, age is expressed as a fraction of longevity in order to calculate curves of expected survival rates for marine mammals of differing lifespan. We followed their methods to calculate three survival rate curves for Hector's dolphin (Fig. 1), as explained in section 2.

The survivorship curve model was used to explore the fluctuations expected in a population after a change in survival rates, for example through conservation management. Specifically, we were interested in the likely events in the Hector's dolphin population in the Pegasus Bay-Canterbury Bight area following the creation of a Marine Mammal Sanctuary.

Two simulations were carried out. Each simulation starts at the time of the introduction of regulations which either reduce the annual entanglement rate to 5% or zero, and follows changes in size and growth rate of the population. Both simulations used the most optimistic values for age at first reproduction (7 years) and calving interval (2 years). Survival rate curve B (Fig. 1) was used for baseline survival rates, from which entanglement rates were subtracted where appropriate. Curve B (Fig. 1) allows for moderate population growth while maintaining a realistic age structure. It is assumed that the Hector's dolphin population had an age structure similar to this in the days before the introduction of modern monofilament gillnets.

The two simulations differ in the starting age distribution used and the selectivity of gillnet mortality (see below). The age distribution of a sample of entangled dolphins would be expected to reflect both the underlying age distribution of the population and any selectivity of gillnets in taking individuals of different age groups. The effect of gillnet entanglement on the population

would depend on the relative contribution of these two factors. We studied the age distribution of a sample of female Hector's dolphins killed in gillnets in the Pegasus Bay-Canterbury Bight area (Fig. 2) to assess the likely effect of entanglement mortality on different age-classes, and to gain information about the likely age distribution of the population. We used the age distribution of females only, because the Leslie Matrix models consider only females. We concentrated on the Pegasus Bay-Canterbury Bight population because the proposed conservation measures will affect this population and we wanted to avoid any differences in age distribution or gillnet selectivity which may exist between populations.

The sample of gillnet-caught dolphins suggested an over-representation of individuals less than 4 years old. As female Hector's dolphins have one calf every 2 to 3 years (Chapter 2), the five newborn females in Fig. 2 would be expected to be associated with at least 20 mature females. Only two mature females are included in Fig. 2. The two simulations explored the effect of a population age distribution with relatively large numbers of young individuals, and gillnet entanglement with a selectivity of this kind, respectively.

In simulation 1, the incidence of gillnet entanglement is assumed to affect all age-classes equally, and the ages of individuals caught in gillnets are assumed to reflect the age distribution of the population at the time the sample was taken. Lockyer et al. (1988a) calculated survival rates for *C. commersonii* assuming that their gillnet-caught individuals were a random sample of the population. The assumption that gillnet entanglement affects all age-classes equally specifies both gillnet selectivity and the age distribution of the population. Simulation 1 starts with an age distribution based on the sample of gillnet entangled dolphins, and the 5% entanglement rate reduces the baseline survival rate of all age-classes by 5%.

Simulation 2 assumed that gillnets were selective with respect to age. If survival rate curve B (Fig. 1) and its corresponding age distribution are taken as the baseline conditions, one would expect 15 years of selective mortality on younger individuals to result in a survivorship regime and age distribution similar to the one corresponding to survival rate curve A (Fig. 1). In simulation 2, the number of individuals in each age-class in the sample of gillnet-caught females was used to determine the reduction in survival rate for that age-class. This was done using a population age distribution in equilibrium with survival

rate curve A. The reduction in survival rate for each age-class caused by a 5% entanglement rate was calculated by dividing the number of entangled individuals in the sample by the expected number of individuals of that age in a population twenty times the size.

2. Input values

Fertility rates

A study of ovaries and uteri indicated that female Hector's dolphins have their first calf when 7 to 9 years old (Chapter 2). No evidence was found for a post-reproductive period, as has been found in pilot whales (Marsh and Kasuya 1984). Field data on photographically identified individuals indicate that female Hector's dolphins have one calf every 2 to 3 years (Chapter 2). The fertility rate of mature age-classes is given as the number of female offspring born per year per female, multiplied by the relevant adult survival rate (as explained in section 2.1). Ages at first reproduction of 7, 8 and 9, and calving intervals of 2 and 3 years are used in the models. Thus in our modelling we used f_x values of 0.25 and 0.16667 times the adult survival rate for a calving interval of 2 and 3 years, respectively, and began with these fertility rates at ages 7, 8 and 9, respectively.

Longevity

Analysis of tooth sections (Chapter 1) showed that the oldest of 33 female Hector's dolphins was 19 years old, and the oldest of 27 males was 20 years old. No rigorous demographic definition exists for longevity, and it is often taken as the maximum age ever recorded for a species (Altman and Dittmer 1972). We have followed this approach, and used 20 year-classes in the population models, with a zero survival rate in the 21st year. Alternative definitions of longevity in population models include the 99th or 98th percentile of the age distribution of a sample, as used by Barlow and Boveng (In press) and Reilly (1984) respectively. Thus, in Barlow and Boveng's (In press) models, one percent of a sample would be older than the age they define as longevity.

Survival rates used in the Reilly-Barlow model

A lower limit to the adult survival rates is provided by survival rate estimates from free-living populations of Hector's dolphins, and the closely related Commerson's dolphin, the only other *Cephalorhynchus* species for which an estimate is available. Annual survival rates for adult Hector's dolphins of 0.797

to 0.865, averaged over all age-classes over 1 year old, are based on a photographic catalogue compiled by Slooten and Dawson between 1984 and 1988 (Chapter 5). Lockyer et al.'s (1988a) estimates of survival rates for *Cephalorhynchus commersonii* were calculated from the age distribution of a sample of 136 individuals which apparently had been killed in gillnets. They estimated annual survival rates as 0.855 for all age groups between 0 and 18 years inclusive, 0.869 for 1 to 18 years inclusive, 0.914 for 6 to 18 years and 0.673 for 0 to 5 years inclusive. The survival rate estimates for both species include deaths from natural causes (including disease and predation) and gillnet entanglement.

Upper limits to the range of survival rates considered in the Reilly-Barlow computations are based on Barlow's (1986) model for *Phocoena sinus* and Reilly and Barlow's (1986) model for longer-lived dolphin species. Barlow used a maximum non-calf survival rate of 0.90 for *P. sinus*, with a maximum observed age of 15 years old, and Reilly and Barlow used a maximum non-calf survival rate of 0.97 for their delphinid model with a maximum age of 50. To fully explore the maximum limits to the growth rate of Hector's dolphin populations, we have used non-calf survival rates up to 0.95.

Reilly and Barlow (1986) and Barlow (1986) generated an upper limit on calf survival rates by assuming that a calf is absolutely dependent on its mother for the first year of its life. Even if a calf has no more than the same risk of dying as an adult, it has the additional risk of dying of starvation if its mother dies before completing one year of lactation. Therefore, the square of the adult survival rate is used as an upper limit on calf survival. The lower limit on calf survival rates was chosen as 0.50, a value typical of pinnipeds (Smith and Polacheck 1981) and long-lived terrestrial mammals (Spinage 1972). We have used the same limits to calf survival in this study.

Survival rates used in the survivorship curve model

Where the Reilly-Barlow model uses one value for s_1, and one constant value for s_2 to s_{20}, the survival curve model uses a different survival rate for each age-class in the transition matrix. We have formulated expected age-specific survival rates for Hector's dolphin, based on the survival rate parameters presented by Barlow and Boveng (In press). In this model the total risk of mortality at a given age is expressed as the sum of a decreasing risk due to juvenile mortality factors, an increasing risk due to senescent mortality factors,

and a constant risk of mortality which affects all individuals regardless of their age. Thus, the probability of survivorship from birth to age x is expressed as:

[3] $$l(x) = l_j(x) \cdot l_c(x) \cdot l_s(x)$$

where $$l_j(x) = \exp [-\beta_1 \cdot \{1 - \exp(-\beta_4 \cdot x)\}]$$
$$l_c(x) = \exp [-\beta_2 \cdot x]$$
$$l_s(x) = \exp [\beta_3 \cdot \{1 - \exp(\beta_5 \cdot x)\}]$$

The survivorship component l_c represents the constant risk of mortality experienced by all age-classes. The survivorship components l_j and l_s represent the independent risks of mortality due to juvenile and senescent factors, respectively. Barlow and Boveng (In press) provided maximum-likelihood estimates of survival rate parameters β_1 to β_5 for marine mammals, based on northern fur seals and human females, as well as a modified version of the fur seal model in which the juvenile and constant mortality parameters β_1 and β_2 were halved (Table 1). In Barlow and Boveng's (In press) survivorship model, age is expressed as a fraction of longevity in order to calculate curves of expected survival rates for marine mammals of differing lifespan. We calculated three survival rate curves for Hector's dolphin (Fig. 1), based on the mortality parameters in Table 1.

Table 1. Maximum-likelihood estimates of survival rate parameters for northern fur seals and human females, with permission from Barlow and Boveng (In press).

Species	ß1	ß2	ß3	ß4	ß5
Northern fur seal (female)	1.3981	0.1710	0.00181	10.259	6.6878
Northern fur seal (modified*)	0.6990	0.0855	0.00181	10.259	6.6878
Human female	0.1302	0.5206	0.00047	141.530	8.7543

* by halving the first two survival parameters ß1 and ß2.

Figure 1. Survival rate curves calculated from Barlow and Boveng's (In press) mortality parameters, based on seal data (curve A), modified seal data (curve B) and human survival rate curves (curve C). Curves A and B converge after age 7.

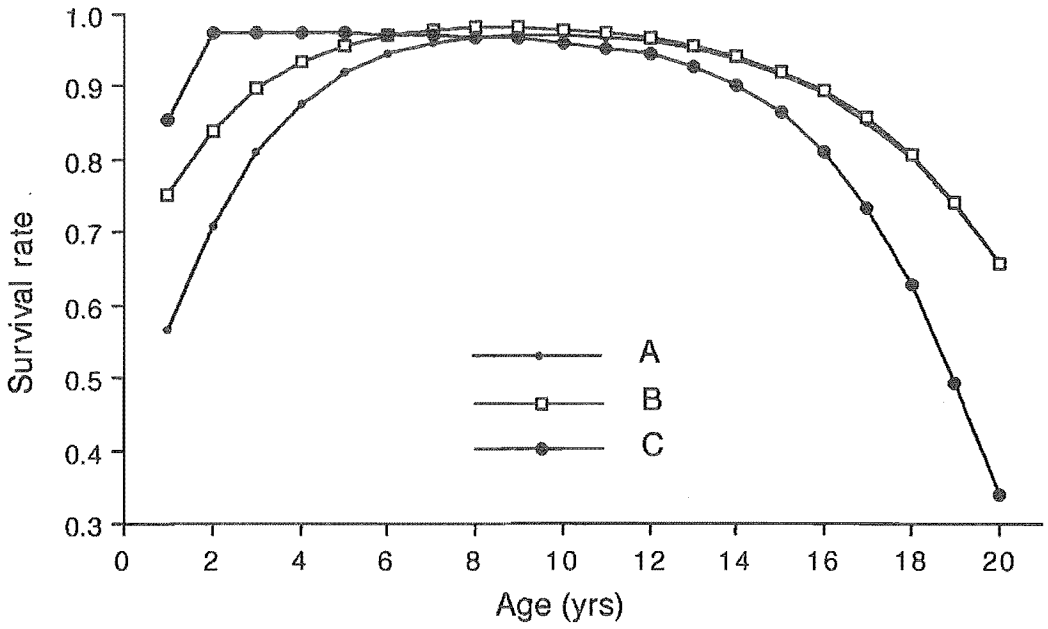
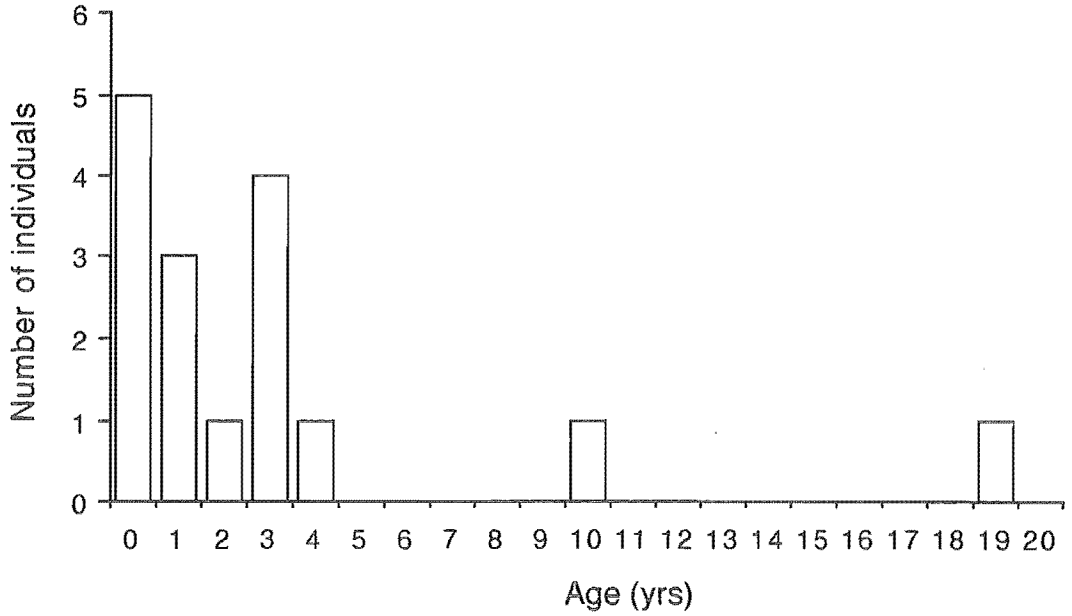


Figure 2. Age distribution of a sample of female Hector's dolphins killed in gillnets in the Pegasus Bay-Canterbury Bight area.



Results

The Reilly-Barlow model

Only constant non-calf survival rates greater than or equal to 0.92, combined with the most optimistic reproductive parameters, resulted in a growing population (Fig. 3). "Best case" projections suggested that maximum population growth rates of 4.4% would be possible for Hector's dolphin populations with constant non-calf survival rates of 0.95, an age at first reproduction of 7 years old, and the most optimistic fertility values. An increase in the age at first reproduction to 9 years, reduces this maximum population growth rate to 2.3%. These are the equilibrium growth rates, associated with a stable age distribution.

Survival rates estimated from free-living populations of Hector's dolphins and Commerson's dolphins, including both natural and net-entanglement mortality, consistently resulted in decreasing populations and can be seen as a "worst case" scenario. The resulting population growth rates may be compared with those corresponding to survival rate curve A (Fig. 1), which also resulted in a decreasing population.

The survivorship curve model

The survivorship curve models using the most optimistic reproductive parameters yielded maximum population growth estimates of -4.2%, 1.8% and 4.1% for survival rate curves A, B and C, respectively. These maximum population growth rates are similar to the maximum growth rates from the constant survival rate model with non-calf survival rates between 0.90 and 0.95. The percentage of a cohort surviving to the maximum age (20) was 5%, 11% and 3% for survival rate curves A, B and C respectively. In this respect the survivorship curve models were more realistic than the constant survival rate models with 11%, 22% and 34% surviving to the maximum age at constant non-calf survival rates of 0.90, 0.93 and 0.95 respectively.

Mean survival rates after the first year of life were 0.89, 0.92 and 0.93 for curves A, B and C respectively, compared to 0.88, 0.91 and 0.93 for the constant survivorship model with non-calf survivorship of 0.90, 0.93 and 0.95 respectively. These average survival rates were calculated by comparing the number of individuals 1 year old and older in a given year with the number of those individuals (now over 2 years old) still alive the next year. This is analogous to following a group of identified individuals in the field and

Figure 3. Contours of percentage population growth rate, as a function of calf and non-calf survival rates. Each panel represents a different combination of age at first reproduction (AFR) and calving interval (CI). The diagonal of each panel shows the upper limit of calf survival rate (the square of non-calf survival, see methods).

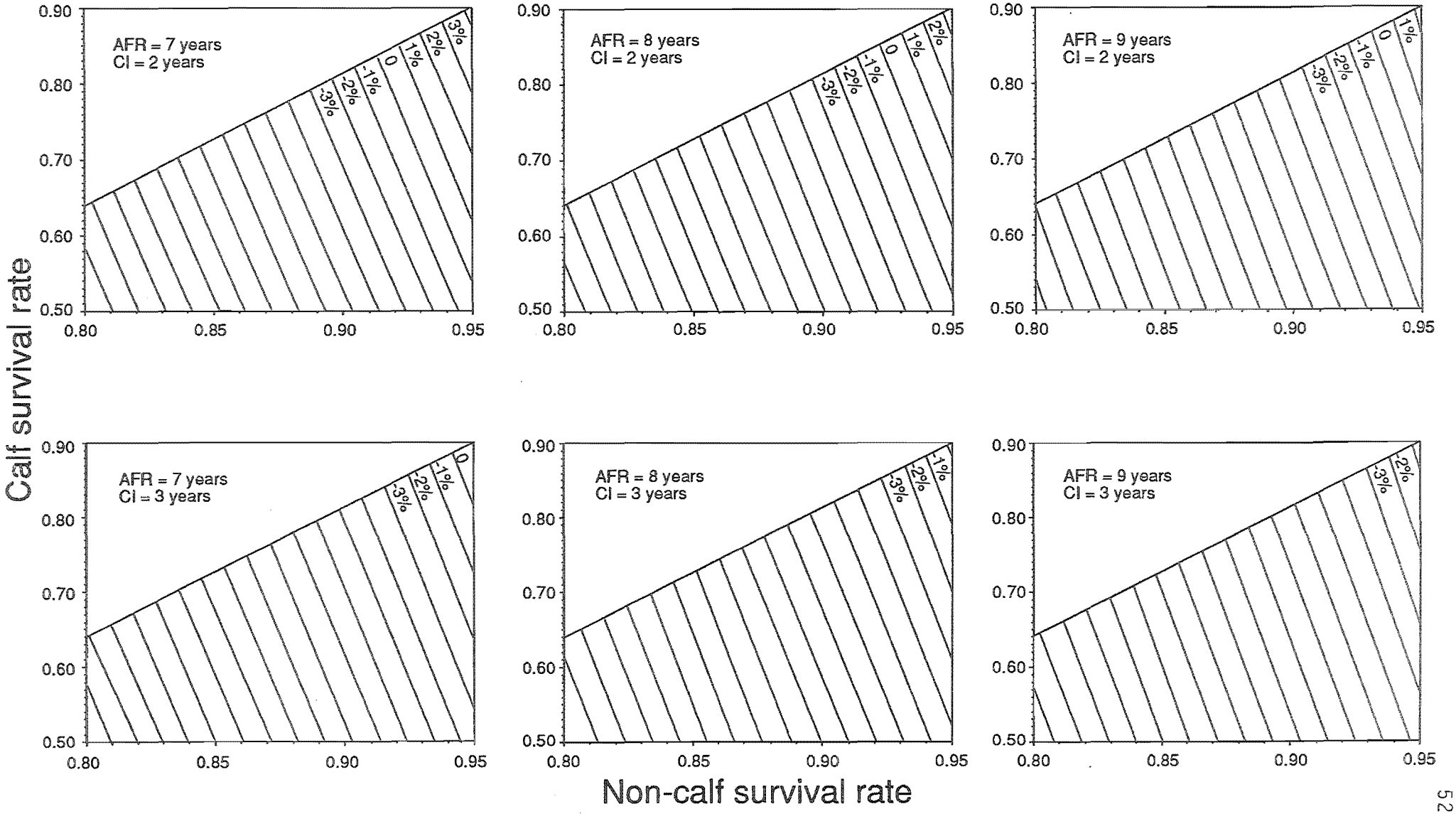
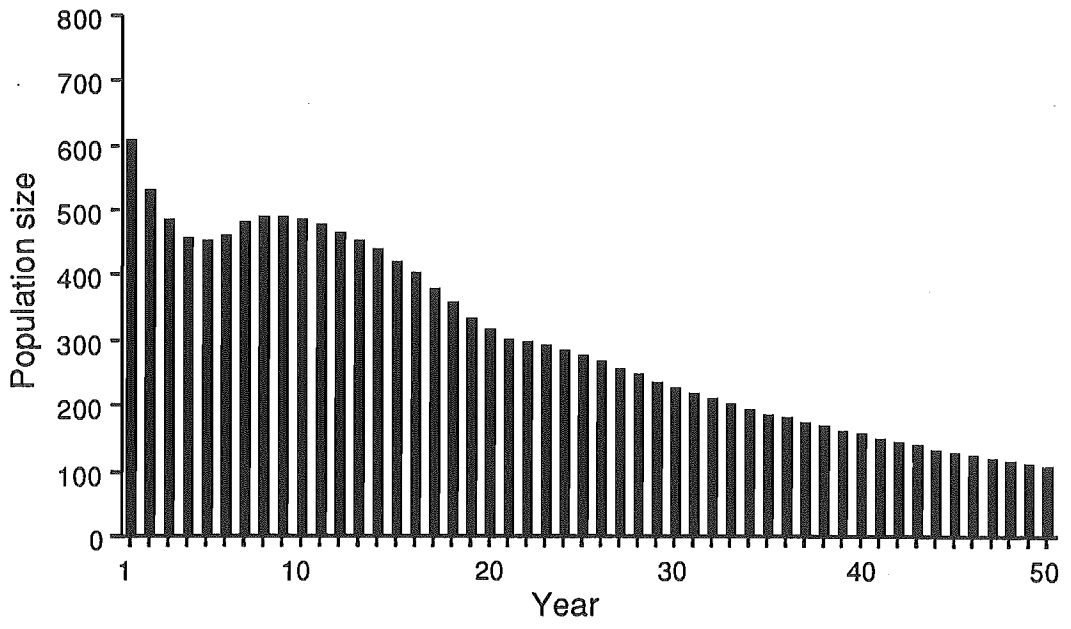


Figure 4. Size (a) and growth rate (b) of a population with an age distribution similar to the sample of gillnet-entangled dolphins in Fig. 2, subject to 5% gillnet entanglement applied equally to all age-classes (simulation 1).

(a)



(b)

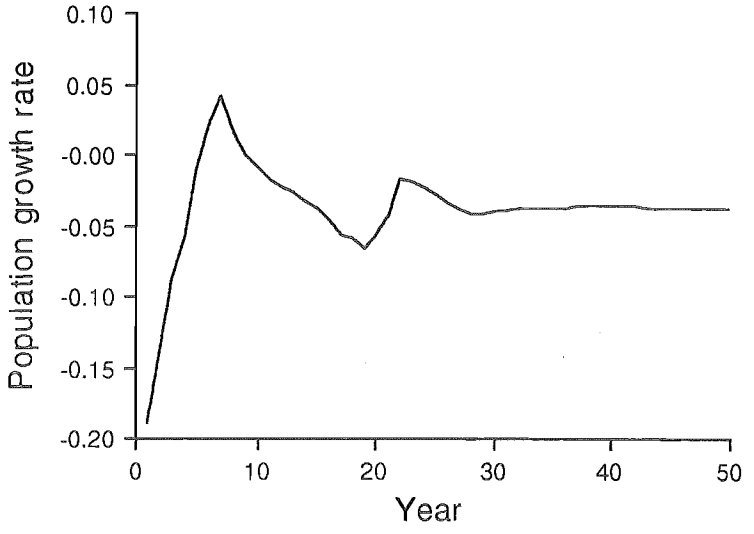
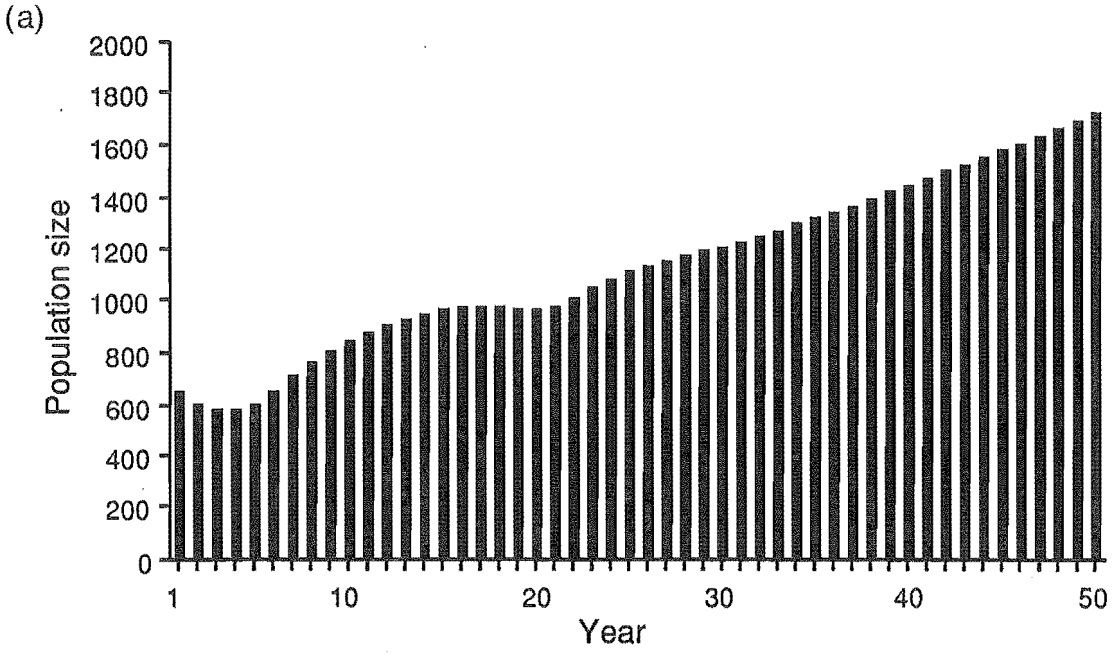


Figure 5. Size (a) and growth rate (b) of a population with an age distribution similar to the sample of gillnet-entangled dolphins in Fig. 2, without gillnet entanglement (simulation 1).



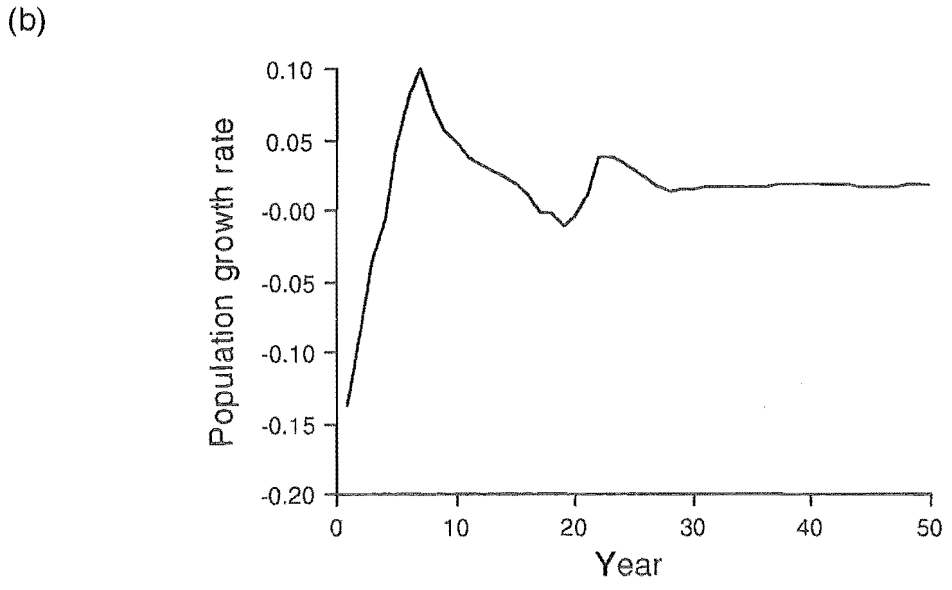
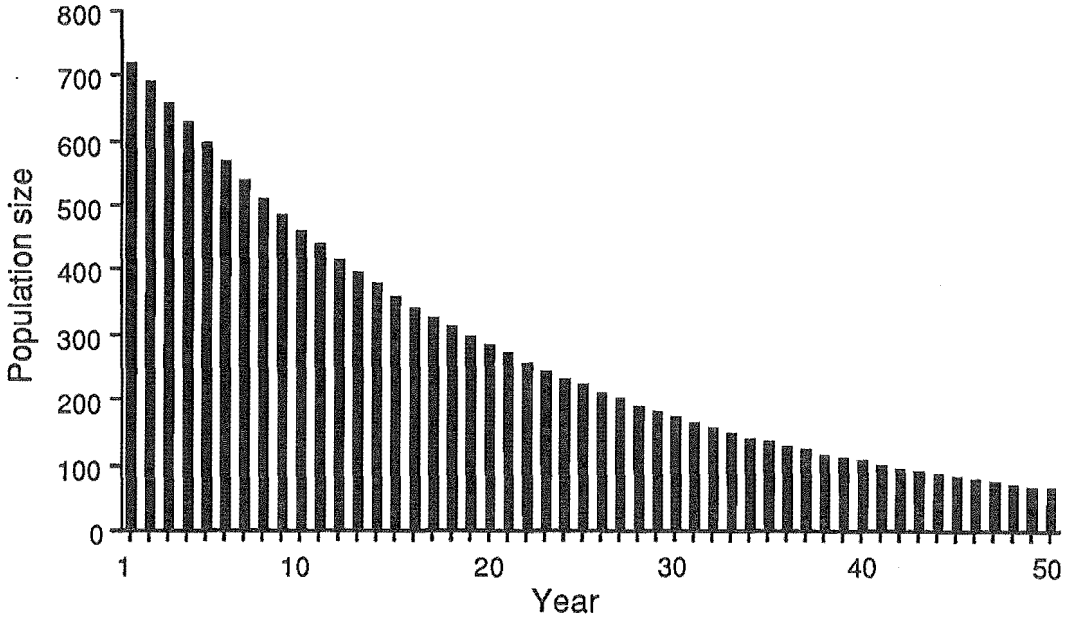


Figure 6. Size (a) and growth rate (b) of a population with an age distribution corresponding to survival rate curve A, subject to 5% gillnet entanglement with a selectivity based on the sample of gillnet-entangled dolphins (simulation 2).

(a)



(b)

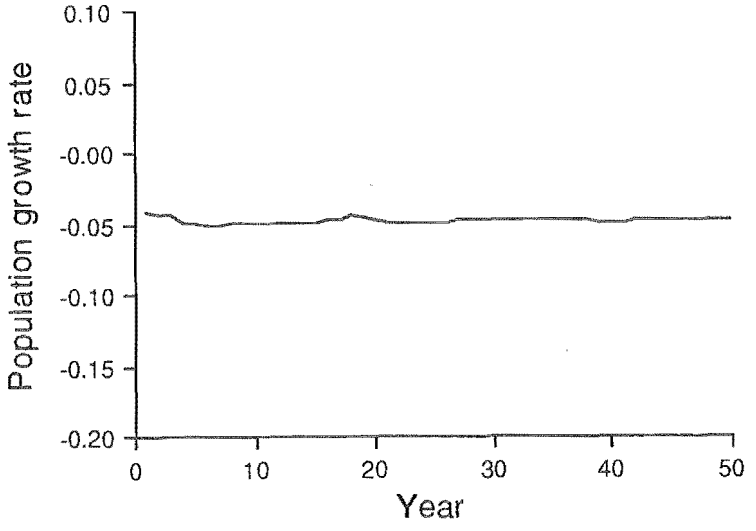
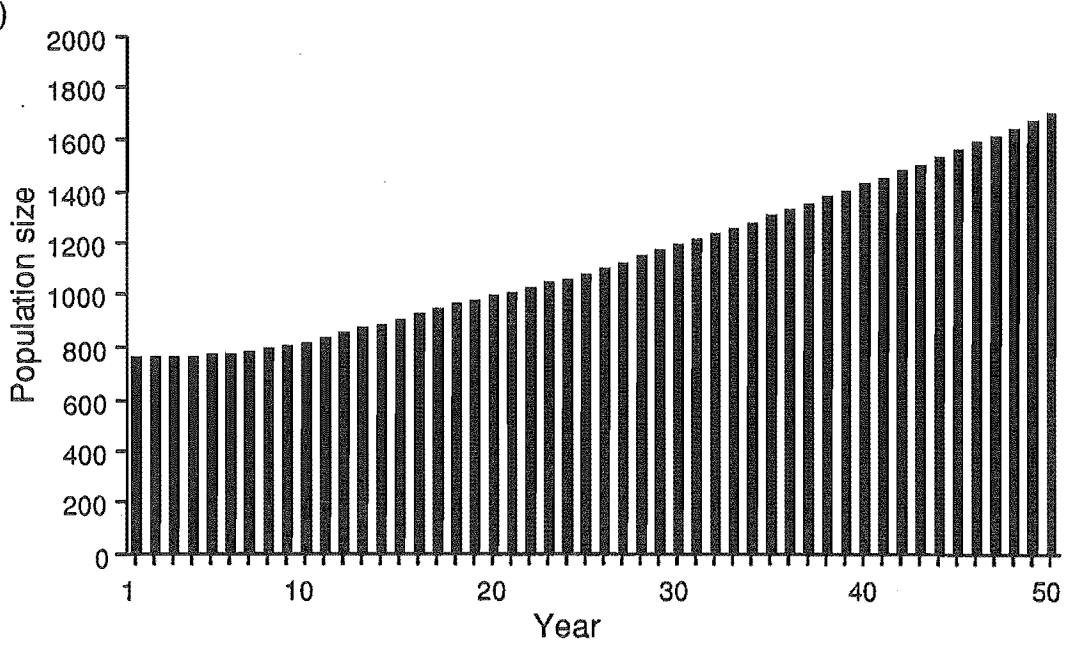
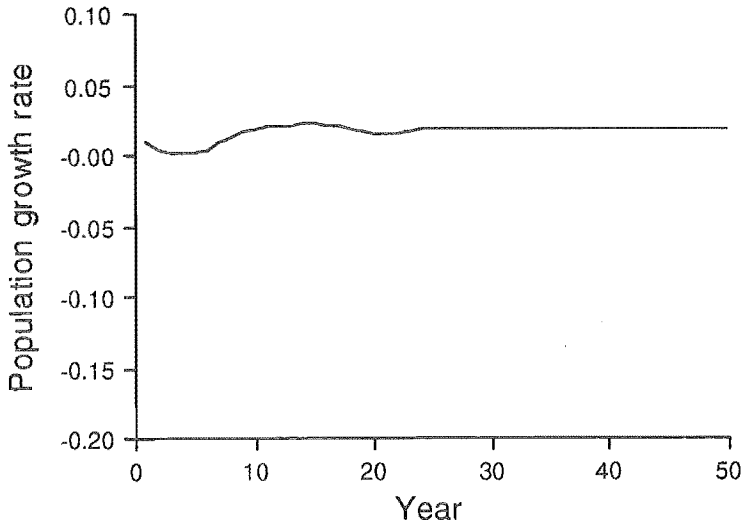


Figure 7. Size (a) and growth rate (b) of a population with an age distribution corresponding to survival rate curve A, without gillnet entanglement (simulation 2).

(a)



(b)



recording the number still alive the next year, as was done in field studies of Hector's dolphin (Chapter 5).

In both entanglement simulations the population growth rate fluctuated for approximately three decades before stabilizing. These fluctuations were more pronounced in simulation 1 (Figs. 4b and 5b) than in simulation 2 (Figs. 6b and 7b). In simulation 2, population size showed a gradual decrease after gillnet entanglement rates were reduced to 5% (Fig. 6a), and a gradual increase after entanglement mortality was eliminated (Fig. 7a). In contrast, population size tended to increase and decrease alternately before reaching a stable rate of change in simulation 1 (Figs. 4a and 5a).

Discussion

The range of population growth rates calculated here indicates that Hector's dolphin has a low potential for population increase. Only constant non-calf survival rates greater than or equal to 0.92, and the two most optimistic age-specific survival curves, result in a growing population. Maximum population growth rates were estimated at 1.8 to 4.4%.

Maximum population growth rates for cetaceans are generally very low (Barlow 1986; Reilly and Barlow 1986), and the population models described here indicate that Hector's dolphin is typical in this regard. The females of other dolphin species reach sexual maturity at around 6 to 12 years, and give birth every 2 to 4 years (Reilly and Barlow 1986; Perrin and Reilly 1984). Data from Hector's dolphins are consistent with this general delphinid pattern. The relatively short lifespan of Hector's dolphins (Chapter 1) means that their expected population growth rates are likely to fall at the lower end of the range calculated by Reilly and Barlow (1986) for dolphins in general. Reilly and Barlow's (1986) model arrived at a maximum population growth rate of 9%, using a maximum longevity of 50 years based on current estimates of longevity in the larger delphinids.

Because age-specific survival rates are difficult to estimate, many of the earlier demographic models for marine mammals, like the Reilly and Barlow (1986) model, have used a constant survival rate across several age-classes. While these models usually use a lower survival rate for juveniles, they do not include a lower survival rate for the oldest age-classes. Despite the obviously

unrealistic assumption of no senescent decline, such models can provide useful estimates of the upper limits to population growth rates (Goodman 1984). However, more realistic models which vary survival rates throughout the lifespan are essential for providing tenable information about the expected age structure of the population, and for modelling changes in age structure and population growth rate caused by changes in survival rates. A decrease in survival rates caused by gillnet entanglement, for example, not only decreases the population growth rate directly, but it also changes the age structure of the population.

Barlow (1987) and Barlow and Boveng (In press) modelled populations of marine mammals, using curves of survival rates similar in structure to those found in fur seals and humans. They chose to use a human survival rate curve to represent the maximum survival possible in a protected environment (Barlow and Boveng In press). Few marine mammals would ever find themselves in such a protected environment, and Barlow and Boveng pointed out that this shape reflects an absolute limit to the likely survivorship of any wild population of marine mammals. Thus the maximum population growth rates based on the human survival rate curve (4.1%), and the constant survival rate model with 0.95 adult survival (4.4%), give an indication of the potential for population growth under ideal conditions. Survival rate curve B, with its 1.8% population growth rate, represents a more likely "best case" scenario.

Entanglement simulations based on the survival rate curve model explored the likely effects of gillnet entanglement, and showed that the results depended on whether the age distribution of the population or the selectivity of gillnets makes a greater contribution to the age distribution of gillnet-caught dolphins. Because of the recent declaration of a Marine Mammal Sanctuary around Banks Peninsula, the recovery of the Hector's dolphin population after a period of gillnet entanglement is of particular interest.

Both simulations indicated that population growth rates were likely to fluctuate after a change in survival rates. Trends in population size and growth rate did not appear to be strongly affected by the selective entanglement used in simulation 2. However, simulation 1 showed that a population age distribution biased towards younger individuals would cause a great deal of fluctuation in both population size and growth rate. The population went through "baby boom" fluctuations for a lengthy period before a new stable population growth

rate was reached, regardless of whether the population was increasing or decreasing. This effect was caused by the peak of young individuals travelling along the age distribution, and causing another peak of young individuals when they reproduced.

In populations with a bias towards younger individuals, short-term monitoring may incorrectly suggest that the population is increasing when it is decreasing in the long-term. If the population is suspected to have an age structure of this kind, it becomes even more important than usual to monitor the population long-term before drawing conclusions about the effectiveness or otherwise of the conservation management scheme. Of course our models show a simplified situation. Entanglement rates tend to fluctuate with changes in the fishing industry, making the situation still less predictable, and making it even more important to be conservative.

The equilibrium growth rate is the rate at which the population would increase if it had the stable age distribution appropriate to the specified schedule of age-specific survival and fertility. It reveals the population's current capacity to increase, and shows what the population growth rate would become if current fertility and survival rates remained constant (Caughley 1977). In nature, however, age distributions are seldom stable (Caughley 1977). The actual population growth rate usually differs from the equilibrium growth rate, because fluctuating food abundance, predator levels and other environmental conditions often change survival rates and reproductive rates. Populations subject to incidental fishing mortality are especially unlikely to reach a stable age distribution as fishing pressures, on the dolphin population and its food resources, change with human food demands, market prices and the dynamics of the fish populations.

Reilly and Barlow (1986) cautioned that the highest rates of increase calculated in their model might be unachievable by any wild dolphin population, as trade-offs may exist between survival and reproduction. It is clear that dolphins (and other animals with similar life-histories) can decrease in number much faster than they can increase (Reilly and Barlow 1986). Besides incidental catches in the fishing industry, other catastrophic events such as pollution, disease, or sudden changes in predator and prey abundance may lead to the rapid extinction of a population. The recent epidemic of phocid distemper virus killing seals and other marine mammals in

the Eastern Atlantic (Pearce 1988) is an example of a sudden population decrease which could not be predicted from population models. Changes in the age distribution of the population caused by changing survival rates can add to the unpredictability of such events.

Gillnet entanglement affects coastal dolphin and porpoise species worldwide (Hofman 1990), and they are ill-suited to cope with this type of mortality due to their generally low reproductive rates. Our calculations suggest that the long-term survival of Hector's dolphin populations is uncertain unless mortality from gillnetting can be substantially reduced if not eliminated. The "worst case" projections support this conclusion, as all survival rates calculated from populations subject to gillnet entanglement result in population decline. Survival rate estimates from free-living populations of Hector's dolphin and Commerson's dolphin subject to natural and net-entanglement mortality consistently resulted in decreasing populations, suggesting that Hector's dolphin and Commerson's dolphin populations are unable to maintain themselves under recent levels of net entanglement. Survival rates need to be around 5 to 10% higher than observed in populations subject to gillnet entanglement, to allow for population growth.

Section II. Photographic identification of individuals

Chapter 5
Survival rates of photographically identified Hector's dolphins

Abstract

Standard photographic identification techniques were used to estimate survival rates in a free-living population of Hector's dolphins. As individuals were identified mostly from injuries to the dorsal fin, the photographic catalogue contained very few young individuals. Our analysis included no newborn calves or yearlings, and provided estimates of survival rates after the first year of life. Average annual survival rates for Hector's dolphins were estimated at 0.797 to 0.865. The estimates came from a population which was subject to relatively heavy mortality from gillnet entanglement, and included natural and net-entanglement mortality.

Introduction

The ability to identify individuals is essential for many biological studies, especially those of behaviour and population biology. Artificial tagging, once considered a necessity in such studies, is being at least partly replaced by recognition of individuals from their natural markings (Würsig and Jefferson In press).

Most free-living animals acquire distinctive marks through injury, such as torn ears, damaged tails or dorsal fins, scars and stiff limbs, and in many species differences in colour pattern are sufficiently distinctive to identify individuals. Individual zebras, for example, are uniquely identifiable from their stripes (Petersen 1972). Natural markings and injuries have been used to identify individuals for a wide range of species, including elephants (Douglas-Hamilton 1973), lions (Schaller 1972), Bewick's swans (Scott 1978; Bateson 1977), fish (e.g. Myrberg and Gruber 1974), frogs (Newman 1977) and rock lobsters (MacDiarmid In press).

Identifying animals from naturally occurring features can be difficult, requiring patience and practice (Pennycuick 1978). However, because it minimizes suffering and disruption of the behaviour of the study animals, it is often the

by: Elisabeth Slooten, Stephen Dawson and Frank Lad

method of choice in studies of behaviour and survival rates (Martin and Bateson 1986).

Photographic identification of naturally identifiable individuals is now a standard research method in studies of whales and dolphins (e.g. Würsig and Jefferson In press; Hammond et al. In press). Besides providing information about associations between individuals (e.g. Würsig 1978; Shane 1980), photographic identification has been used to calculate key population parameters such as calving rates, survival rates and population size (e.g. Bigg 1982; Hammond 1986).

In this study, individual Hector's dolphins were photographically identified to gain insights into their population biology (this chapter) and their social organization (Chapter 6). Here, survival rates for a free-living population of Hector's dolphins were calculated from a photographic catalogue compiled over 1984 to 1988 by Slooten and Dawson.

Methods

In photo-ID studies of dolphins, the trailing edge of the dorsal fin is the most commonly used identifying feature, as it tends to damage relatively easily (Würsig and Jefferson In press). Most Hector's dolphins in our catalogue were identified from injuries to the dorsal fin. A smaller proportion were identified from body scars or unusual body coloration.

Field methods

We took over 23,000 photographs of Hector's dolphins. Most were taken with a motor-driven 35mm camera equipped with a data-back showing time and date, and with 50mm (f 2.8) or 85mm (f1.4) lenses. To minimize any blurring effect of movement, all photographs were exposed at shutter speeds of 1/500 or 1/1000s. Because Hector's dolphins are essentially black, white and grey, we made extensive use of black and white film (Kodak Tri-X or Kodak TMax 400). We used a limited amount of colour film (Kodachrome 64) to record fresh scars. Identifiable individuals were chosen from proofsheets using a 10x loupe, and 9x14cm prints made for comparison and filing. All photographs were taken from a 3.9m outboard-powered inflatable boat. Whenever we encountered dolphins we attempted to photograph all distinctive individuals in the group.

We conducted photographic identification surveys in the inshore waters off Banks Peninsula, New Zealand. Being at the centre of the study area, Akaroa Harbour (43° 50'S; 172° 56'E) and the nearby waters of the south side of the peninsula were most frequently surveyed (Fig. 1 and Table 1). Because fieldwork was concentrated during the summer period, effort and re-sightings were listed by season, '84-'85 referring to 1 July 1984 to 30 June 1985.

Filing the photographs

Photographs of distinctive individuals were filed into a catalogue referenced to a computer database of sighting information. Individuals were numbered according to the position and type of nick(s) on the dorsal fin or to the position and type of pigmentation markings or body scars. To ease comparisons, similar individuals were filed together in the photographic file.

We categorized individual dolphins according to how obvious their identifying marks were. Category 1 individuals were those whose marks were so obvious they were very unlikely to have been missed in the field, and had an excellent chance of being identified from photographs after each encounter (Fig. 2). Of the 65 individuals in category 1, three were identified from very large body scars, 11 from extensive pigmentation differences, and one on the basis of abnormal fin shape. The remaining 47 were identified from extensive nicks and other injuries to the dorsal fin. To estimate survival rates we used only the 59 category 1 individuals who had been sighted at least once in Akaroa Harbour, the most frequently surveyed part of the study area.

Category 2 individuals also had obvious identifying marks, and were very unlikely to be mis-identified from good photographs, but were more likely either to go unnoticed in the field, or were more difficult to identify from photographs taken at less than ideal angles (Fig. 3). Of the 67 category 2 individuals, three were identified from large body scars, eight from pigmentation differences, two on the basis of unusual fin shape, and the remaining 54 were identified from nicks and other injuries to the dorsal fin. Category 1 and 2 individuals were used for analysis of association patterns between individual Hector's dolphins (Chapter 6).

More subtle marks (ID category 3) were useful for distinguishing individuals while observing behaviour or group interactions, but individuals

Figure 1. Map of the study area.

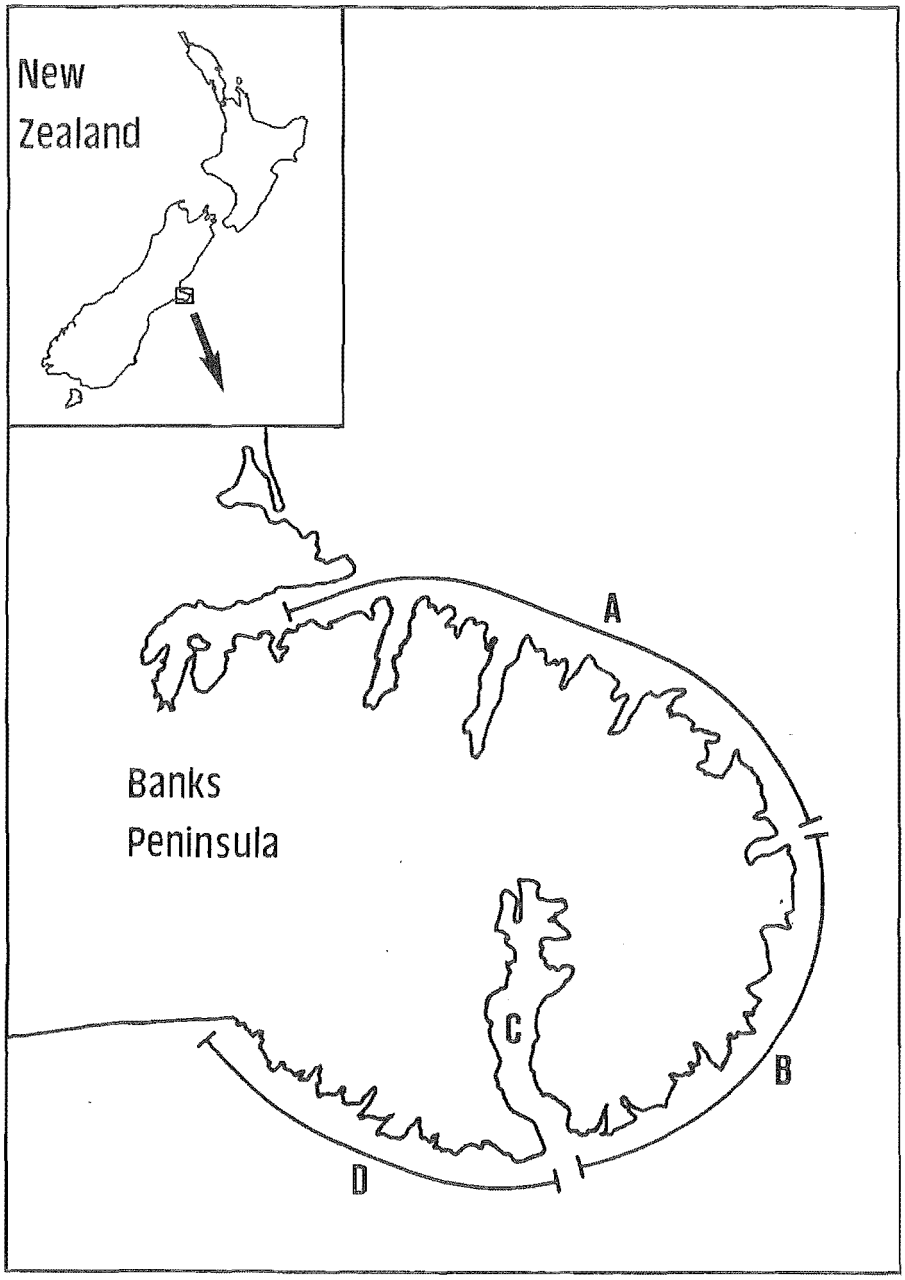


Table 1. Number of fieldwork days spent in each part of the study area.

	'84-'85	'85-'86	'86-'87	'87-'88
A	1	1	3	2
B	5	19	27	15
C	6	71	58	60
D	1	50	31	8
Total	13	141	119	85

Figure 2. Examples of identified individuals in category 1, distinguishable on the basis of dorsal fin nicks (top and middle) and body colouration (bottom). These individuals had obvious distinguishing marks and an excellent chance of being identified from photographs after each encounter. Only category 1 individuals were used to calculate survival rates.

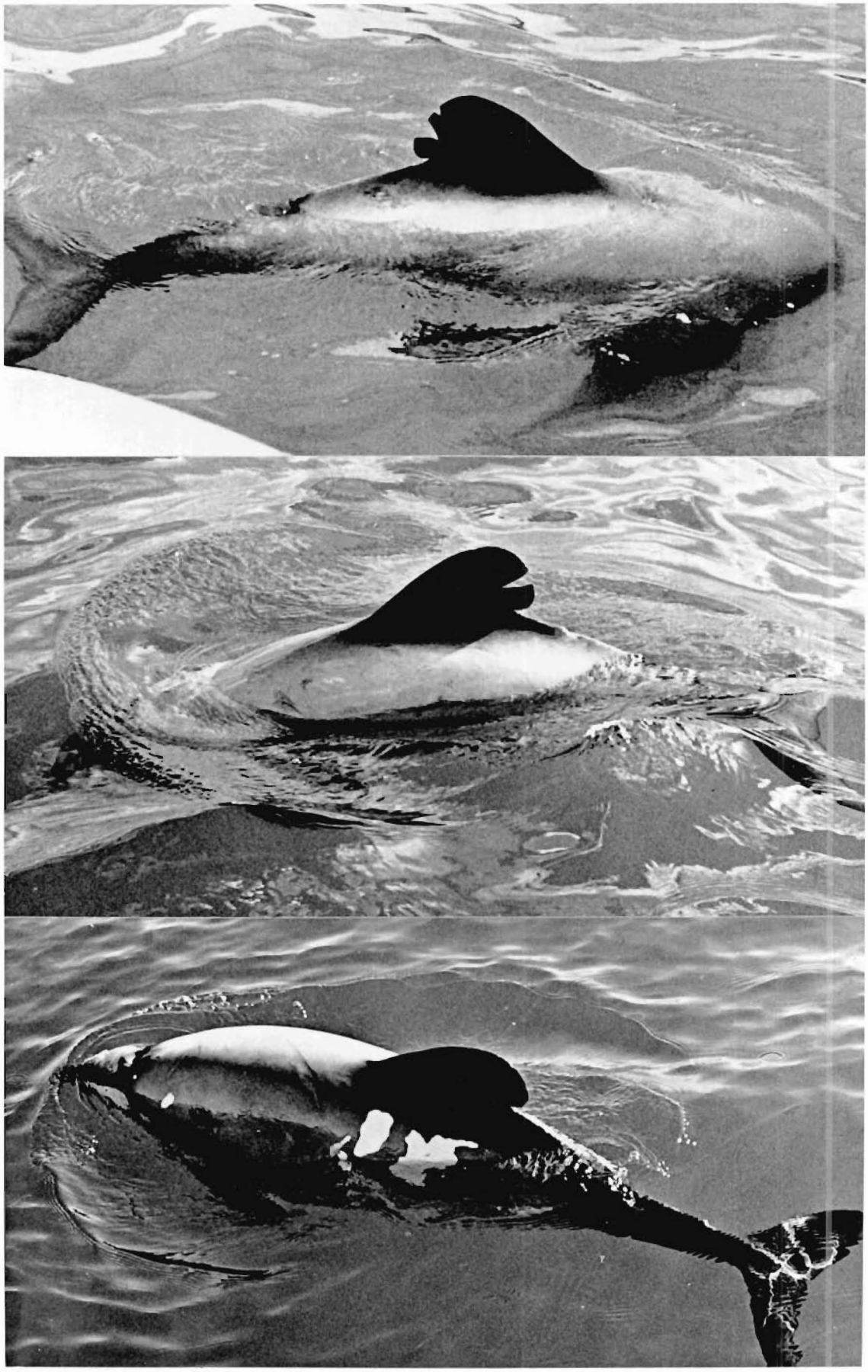


Figure 3. Examples of identified individuals in category 2, distinguishable on the basis of dorsal fin nicks (top and middle) and body colouration (bottom). These individuals were very unlikely to be mis-identified from good photographs, but more difficult (than category 1 individuals) to identify from photographs taken at less than ideal angles. Category 2 individuals were included in the analysis of association patterns (Chapter 6). They were not used for the survival rate calculations in this chapter.

distinguishable only by such subtleties have been excluded from these analyses. Such individuals are too easily missed in the field and are difficult to identify positively from photographs.

Analysis

Sightings data were first divided into 'cohorts', where cohort j is defined as all dolphins first identified in year j. Re-sighting rates were calculated by dividing the re-sightings in a given year by the sightings of the previous year (see Buckland In press). The calculations were made by year rather than cohort, as it was not reasonable to assume a constant survival rate across years. Human impacts on the population are known to have fluctuated markedly across years during the study period.

As in all photographic identification studies, the disappearance of an individual in a given year does not necessarily imply it has died. There are four other possibilities: It could have been (1) not identifiable from the photographs taken, (2) encountered but not photographed, (3) in the area but not encountered or (4) have moved away from the study area, permanently or temporarily.

Possibilities (1) and (2) were reduced substantially by choosing only the most obviously identifiable individuals for analysis. By attempting to photograph each distinctive individual seen in the field we reduced possibility (2). Possibilities (3) and (4) were reduced by using only individuals who had been sighted at least once in Akaroa Harbour, the central part of the study area. We have attempted to estimate possibility (4), the number of disappearances from the catalogue due to movements of individuals away from the study area, by comparing sightings and apparent disappearances from part of the study area (Akaroa Harbour) with sightings from the entire area.

A problem for studies which use sightings records to calculate survival rates is that each individual has a different sighting probability. Individuals which live on the fringe of the study area are a major cause of sighting heterogeneity, as they are sighted less frequently. This problem is worse if each individual is sighted only once every few years, i.e. each individual already has a low sighting probability (e.g. Buckland In press).

Buckland (In press) suggests that sighting probabilities should be at least 0.2 in a given year (i.e. each individual should be seen at least once every 5 years), and that research should continue for many years - ideally at least ten. Such a long-term record of survival rates can then be examined for years in which survival rates are relatively low, and these years can be eliminated from the analysis. Hector's dolphins have a much higher sighting probability than the humpback whales in Buckland's (In press) example, as each individual was sighted at least once every year. However, our study so far spans only four years. We have attempted to solve the problem of sighting heterogeneity by including in the analysis only those individuals who had been sighted in the central part of the study area.

Results

Individual Hector's dolphins identified and re-sighted in the period of 1984 to 1988 are shown by cohort in Table 2. The corresponding re-sighting rates, listed in Table 3, are found by comparing the sightings in one year with the number of those individuals who were re-sighted the next year. As in Buckland (In press), re-sighting rates equal to 1 were based on small numbers of identified individuals.

Table 2. Number of photographically identified Hector's dolphins in each cohort. The first number in each sequence is the number of dolphins first identified in that year. Subsequent years show the number of re-sightings of those individuals.

'84-'85	'85-'86	'86-'87	'87-'88
3	3	3	3
	30	23	16
		17	13
			9

Table 3. Re-sighting rates, calculated by dividing the re-sightings in a given year by the sightings of those individuals in the previous year.

Year	sightings	re-sightings	re-sighting rates
'84-'85	3	-	-
'85-'86	33	3	1.0
'86-'87	43	26	0.788
'87-'88		32	0.744

Table 5. Re-sighting rates calculated from Akaroa Harbour sightings only, by dividing the re-sightings in a given year by the sightings of those individuals in the previous year. The figures in parentheses include sightings outside Akaroa Harbour.

Year	sightings	re-sightings	re-sighting rates
'85-'86	31	-	-
'86-'87	37 (39)	22 (24)	0.7097 (0.774)
'87-'88		26 (28)	0.703 (0.718)

Table 6. Estimated survival rates for the whole study area when the numbers in Table 3 have been corrected for 18% of the disappearances being due to movement rather than death of the individual.

Year	sightings	re-sightings	survival rates
'84-'85	3	-	-
'85-'86	33	3	1.0
'86-'87	44.27	27.27	0.826
'87-'88		33.997	0.768

Table 4 lists the sightings from Akaroa Harbour only, the most comprehensively surveyed part of the study area. Individuals are first listed in Table 4 in the year they were first sighted in Akaroa Harbour. Of the individuals who "disappeared" from Akaroa Harbour, three were seen outside the Harbour after their last Akaroa sighting and are shown in parentheses in Table 4. In the first cohort, two of the nine disappearances between '85-'86 and '86-'87 were re-sighted outside Akaroa Harbour. One of these was re-sighted in '87-'88, again outside the harbour. In the second cohort, one of the six disappearances was re-sighted outside Akaroa Harbour. Thus, at least four of the 22 (18%) disappearances from the harbour were due to movement rather than death. We calculated re-sighting rates on the basis of the Akaroa Harbour sightings, and corrected these for movements by adding the re-sightings of "disappeared" dolphins from other parts of the study area (Table 5).

Based on the assumption that dolphin movements at the edges of the study area are similar to those from Akaroa Harbour, we have applied the 18% correction factor to the data from the whole study area (Table 6). The adjusted annual survival rate for Hector's dolphins (Table 6) was between 0.797 and 0.865, depending on whether the '84-'85 survival rate of 1.0 (based on 3 individuals) was included in the average.

Discussion

Using injuries as the main basis for identification meant that the photographic catalogue contained very few young individuals. There were no newborn calves or yearlings in the category 1 identifications. Therefore our analysis provides estimates of survival rates after the first year of life. The estimates came from a population which was subject to relatively heavy mortality from gillnet entanglement during the study (Dawson, 1990), and included natural and net-entanglement mortality.

It is conceivable for an individual to be injured so severely that it gains a new distinguishing mark but loses the old one. This is highly unlikely for the category 1 individuals, as there are no relevant individuals in the catalogue with injuries large enough to have obscured their old markings. Also, several individuals in the catalogue had more than one distinguishing feature (e.g. a

fin nick and a body scar), and none of these individuals has been injured in such a way as to obscure one of the original marks.

The survival rates calculated here are similar to those of Commerson's dolphin, *Cephalorhynchus commersonii*, the only other species in the genus for which comparable rates are available. Lockyer et al. (1988a) estimated survival rates for Commerson's dolphin from the age distribution of a sample of 136 individuals found beach-cast and presumed killed in gillnets. They estimated an annual survival rate of 0.855 for all age groups between 0 and 18 years inclusive, a rate of 0.869 for 1 to 18 year olds, 0.673 for 0 to 5 year olds, and 0.914 for 6 to 18 year olds.

Survival rate estimates for both Commerson's and Hector's dolphin came from populations which were subject to gillnet entanglement, and the estimates included natural and net-entanglement mortality. When incorporated into a Leslie Matrix population model, survival rate estimates of both species resulted in decreasing populations (Chapter 4), suggesting strongly that recent gillnet entanglement levels have been too high to allow population growth. Fishers seldom comply with the requirement of the Marine Mammal Protection Act (1978) that gillnet entanglements of marine mammals be officially reported (Cawthorn 1988; Dawson 1990). Therefore, entanglement data are not sufficiently detailed to determine what proportion of the mortality rate is due to net entanglement rather than natural losses to predators, old age and disease.

Ongoing photographic identification studies will provide improved information on survival rates and the amount of interchange between local populations of Hector's dolphins. Photographic surveys are now being extended to areas north and south of Banks Peninsula. These data will refine estimates of how many of the individuals who disappear from the Banks Peninsula population have emigrated rather than died.

Chapter 6
Social organization of Hector's dolphins

Abstract

Association patterns of Hector's dolphins were studied using standard photographic identification techniques. Many individually identified Hector's dolphins were sighted in the study area in successive seasons and years, and appeared to be resident in the area. Hector's dolphins from the north and south side of Banks Peninsula were not observed to associate with each other, suggesting they form two separate populations. The social organization of the southern Banks Peninsula population was characterized by relatively fluid association patterns, similar to those of bottlenose dolphins. Both male and female Hector's dolphins interacted with a large number of other individuals, males more so than females. Their association patterns support the hypothesis that Hector's dolphins have a promiscuous mating system.

Introduction

Social organization and behaviour are important aspects of the population biology of a species. The interaction between behaviour, life-history and population biology is of great interest to both evolutionary biologists (e.g. Horn and Rubenstein 1984; Rubenstein and Wrangham 1986) and conservation biologists (e.g. Schaller 1972, 1977; Schaller et al. 1985; Gilpin and Soulé 1986; Lande 1988). Most important for conservation biology, the social and sexual behaviour of individuals may affect the reproductive rate of a population, and may help explain the effects of population size on reproductive rates (e.g Whitehead 1987).

A first step in studying social organization is the identification of individuals. In studies of whales, dolphins and porpoises this is generally done photographically (e.g. Hammond et al. In press; Würsig and Jefferson In press). Photographs of identifiable individuals have provided the basis for studies of a growing number of species, including orca *Orcinus orca* (Balcolm et al. 1982; Bigg 1982), humpbacked dolphins *Sousa chinensis* (Saayman and Tayler 1973, 1979), bottlenose dolphins *Tursiops truncatus* (Würsig 1978; Shane 1980; Wells et al. 1987), dusky dolphins *Lagenorhynchus obscurus* (Cipriano 1985; Würsig and Würsig 1980), spinner dolphins *Stenella*

longirostris (Norris and Dohl 1980), humpback whales *Megaptera novaeangliae* (Katona et al. 1979), sperm whales *Physeter macrocephalus* (Arnbom 1987; Whitehead In press) and right whales *Eubalaena australis* (Payne et al. 1983).

The social organization of Hector's dolphins has been studied by observing their social behaviour (Chapter 7) and individual associations and movement patterns (this chapter). This chapter reports data from an ongoing photographic identification study of Hector's dolphins. Association patterns elucidate the social organization of Hector's dolphins and how it compares with other delphinids, and provide an insight into the likely mate searching behaviours used by Hector's dolphins.

Methods

Field methods, compilation of the photographic catalogue, and definitions of identification categories are described in Chapter 5. Individuals of identification category 1 and 2 (n=132) were used in this chapter. Seventy nine of these had been seen ≥3 times and were used in an analysis of association patterns.

A group was defined as two or more dolphins in close contact (<20 metres from each other) and closer to each other than to individuals belonging to other groups (as in Chapter 7). Hector's dolphins are generally sighted in groups of two to eight individuals. The most common sightings are of several small groups within the same general area. These small groups often merge and split, and appear to have little stability. For this reason, associations of individual dolphins were studied at the 'supergroup' level. A 'supergroup' is defined as a cluster of dolphin groups <200m apart and closer to each other than to groups belonging to other supergroups. We use the term 'population' in the general rather than genetic sense.

Analysis

A half-weight association index (Cairns and Schwager 1987; Wells et al. 1987) was used to calculate the degree of association between individuals.

$$\textit{Association index} = \frac{2x}{(a+b)}$$

where x is the number of joint sightings (scored once for each supergroup) that included both dolphin A and dolphin B, a is the total number of sightings of dolphin A, and b is the total number of sightings of dolphin B. The association index ranges from 0 for two dolphins who are never seen together, to 1 for two dolphins who are always seen together.

We used this index because Cairns and Schwager (1987) found it to be the least biased if pairs are more likely to be scored when separate than when together. In any photographic identification study there are two reasons why the number of joint sightings are likely to be underestimated. Firstly, before two individuals can be scored as sighted together, they must not only both be seen, but also both photographed. Secondly, at least one member of a pair will be located more often when members are separate than when they are together, since if either one of two groups is located the pair can be scored as separate, whereas only one group can provide the information that they are together.

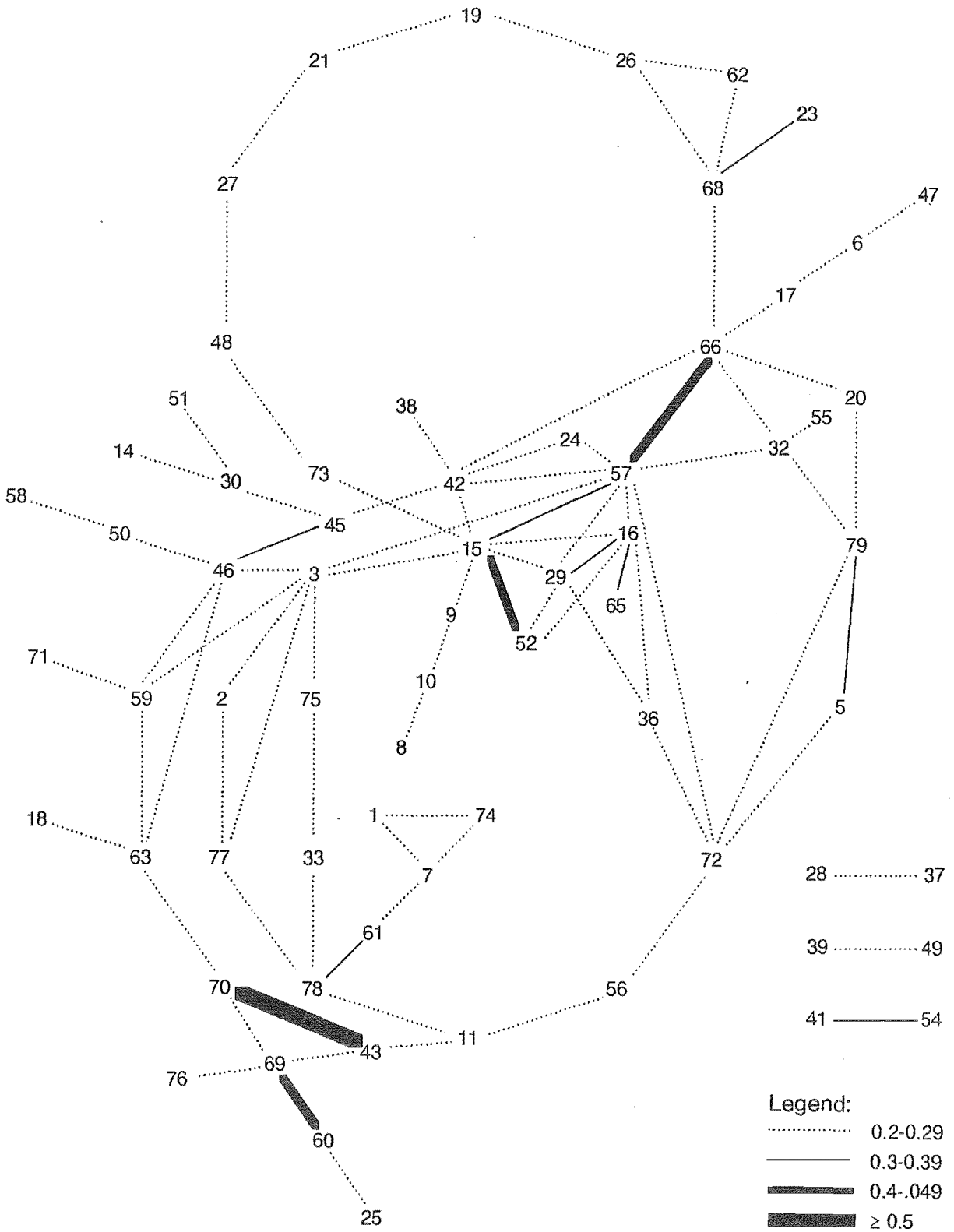
Results

Of the 132 individuals of identification category 1 or 2, 79 were sighted ≥3 times, 53 individuals ≥5 times, 13 individuals ≥10 times, and three individuals ≥15 times. The most frequently sighted individuals (max. = 22 sightings) were seen in each year of the study and in all seasons, suggesting that they were resident in the area.

None of the individuals sighted on the north side of Banks Peninsula (from Lyttelton Harbour to Le Bons Bay) were ever seen on the south side (from Le Bons Bay south), or vice versa (see Chapter 5, Fig. 1). Consequently, individuals from the north and south side of the peninsula were not observed to associate. Even within the southern Banks Peninsula waters, individuals tended to favour particular areas. All 79 individuals used in the association analysis were sighted exclusively on the south side of Banks Peninsula, as none of the category 1 and 2 individuals from the north side of the peninsula were sighted sufficiently frequently to be included in the analysis.

The Hector's dolphins from the south side of Banks Peninsula appeared to be members of a single interacting population. Associations among individuals

Figure 1. Diagram showing all individual associations with an association index ≥0.2.



varied in strength, but overall formed a complex web without clear cut-off points (Fig. 1). The members of this population were never all seen together in a single cohesive group. Rather, they were typically dispersed into a variety of groups and supergroups, distributed around the south side of Banks Peninsula. Associations between individuals were relatively fluid, each individual associating loosely with a large number of other individuals, rather than having a few very close associates. Twenty-one of the 79 individuals used in the association analysis had one or more associations with an index ≥0.3. Only eight individuals had any association indices ≥0.4, and one pair of individuals had an association index ≥0.5.

Males interacted with a greater number of other individuals than females, as one might expected if males search for, rather than monopolize mates. The mean number of associates from the sample of 79 individuals (with a non-zero association index) was 18.0 for males and 12.3 for females ($t = -1.986$, d.f. = 38, one-tailed test, $p < 0.05$). However, the number of relatively close associates (association index >0.2) was similar for males and females (mean for males 2.38, mean for females 2.53; $t = 0.198$, d.f. = 38, one-tailed test, $p > 0.05$). In addition, all individuals interacted with more subtly marked individuals who were not included in the sample analyzed here (ID category 3), and with many unidentified individuals (those lacking distinctive markings).

Discussion

Many of the Hector's dolphins individually identified from Banks Peninsula waters appear to be resident there, having been sighted in the same area in successive seasons and years. Hector's dolphins from the north and south side of the peninsula were not observed to associate with each other, suggesting they form two separate populations. The social organization of the southern Banks Peninsula population was characterized by relatively fluid association patterns.

So, how do Hector's dolphins compare to other species? Among the delphinids, group structure ranges from very stable in orca *Orcinus orca* (Balcolm et al. 1982; Bigg 1982) to relatively fluid in most dolphins (Würsig 1989). The most intensively studied species, orca and bottlenose dolphins *Tursiops truncatus*, illustrate the range of social organization among delphinids. Both species have been studied long-term, with photographic

identification work beginning in the early 1970's and still continuing (Balcolm et al. 1982; Bigg 1982; Irvine et al. 1981; Wells, 1986; Wells et al. 1987; Scott et al. 1990).

Orca resident in the coastal waters of British Columbia and Washington State live in remarkably stable groups or 'pods', which, except for births and deaths, have remained unchanged for the 20 years they have been studied (Balcolm et al. 1982; Bigg 1982). Each pod is a long-term family or kinship group, and appears to be a closed breeding unit.

The social organization of bottlenose dolphins is much more dynamic. Like orcas, the bottlenose dolphins off Sarasota (Florida) form a relatively closed population with a well-defined home range (Wells et al. 1987). Several offspring have remained in the area beyond sexual maturity, and permanent immigration and emigration of members of other age classes is infrequent (Wells et al. 1987; Scott et al. 1990). However, association patterns among the 100 or so Sarasota dolphins are much less stable than in orca, with small groups of regularly recurring associates travelling through their range and frequently joining other groups for periods of minutes or hours. Nearly every female dolphin of the Sarasota population spends some time associating with each other female (Wells et al. 1987).

Spinner dolphins *Stenella longirostris* appear to have even less predictable association patterns. These dolphins are primarily pelagic and, unlike inshore dolphins, often occur in large groups of hundreds or thousands of individuals (Norris and Dohl 1980; Norris et al. 1985; Leatherwood et al. 1988). Spinner dolphin groups appear to be highly dynamic assemblages of variable size and composition, with only small subgroups remaining stable for any length of time (Norris and Dohl 1980; Norris et al. 1985).

The social organization of Hector's dolphins appears to be intermediate between the very stable groups of orca off Vancouver Island (Bigg 1982; Balcolm et al. 1982) and the very fluid social system of spinner dolphins off Hawaii (Norris et al. 1985). Within the Hector's dolphin population on the south side of Banks Peninsula, association patterns were at least as fluid as observed for bottlenose dolphins. Small groups of Hector's dolphins frequently merged and split, and appeared to have little stability. It was common for example to see two groups of four individuals merge and split into

a group of two and a group of six. This instability was reflected in low association indices between individuals.

Clusters of individuals who associated strongly were less evident among the Banks Peninsula Hector's dolphins than among the Sarasota bottlenose dolphins (Wells 1986; Wells et al. 1987). Within the range of known delphinid social systems, Hector's dolphins would seem to be most similar to bottlenose dolphins. Group size and composition are not quite as fluid as in spinner dolphins (Norris and Dohl 1980; Norris et al. 1985), and certainly not as stable as in orca (Balcolm et al. 1982; Bigg 1982).

In both bottlenose dolphin and orca populations, there is some variability in movements and association patterns. This variation appears to be most extreme in orca, which form resident and transient populations which apparently do not interact (Bigg 1982; Baird and Stacey 1988). Transient and resident orca differ in pod size and behaviour, with transient pods ranging further, and forming smaller, possibly less stable groups (Bigg 1982; Baird and Stacey 1988). Morphological differences between transient and resident orca suggest that they may be genetically separated (Baird and Stacey 1988).

A high degree of variability in movement and association patterns may be a feature of most populations of delphinids, and possibly other cetaceans. Some of the Sarasota bottlenose dolphins (Wells et al. 1987), and some of the Hector's dolphins in this study did not appear to form any consistent associations. The more widely ranging individuals may extend the genetic boundaries of populations. Wells et al. (1987) noted that some males ranged over large areas, beyond the regions in which the largest female groups concentrated their activities. A high degree of genetic heterozygosity measured within the relatively small population of Sarasota bottlenose dolphins suggested that it was not a closed reproductive unit (Wells 1986; Wells et al. 1987).

Like bottlenose dolphins and orca, Hector's dolphins appear to be resident in relatively small geographical areas. Continued and further-ranging photographic identification studies, especially to the north and south of the Banks Peninsula area, will provide more information on the discreteness of Hector's dolphin populations. This information will be important in assessing

to what extent human impacts and conservation measures affect local and adjacent populations.

Both male and female Hector's dolphins interacted with a large number of other individuals, males more so than females. Wells et al. (1987) argued that bottlenose dolphins have a promiscuous mating system, on the basis of their fluid association patterns, large testis size and high sperm concentrations. This would appear to be the most likely mating system for Hector's dolphins also. Further evidence for a promiscuous mating system, and its conservation implications are discussed in Chapters 3, 7 and the thesis Discussion.

Section III. Behaviour

Chapter 7
Hector's dolphin behaviour: A sequence analysis

Abstract

Behaviour sequence analysis was used to classify Hector's dolphin behaviour into five categories: 'feeding', 'sexual', 'aggressive', 'play' and 'aerial'. I investigated the relationship between behaviour category and social context for the sexual behaviours. The number of sexual behaviours per individual was highest in groups of 11-15 dolphins, and tended to increase after groups came together. Behavioural data support the hypothesis that Hector's dolphins have a promiscuous mating system in which males move from group to group searching for sexually active females, rather than attempting to monopolize females.

Introduction

Behavioural studies of whales, dolphins and porpoises have tended to focus on broad activity patterns such as foraging, travelling, milling, resting and so on (e.g. Würsig and Würsig 1979, 1980; Shane et al. 1986; Shane 1987, 1990; Jefferson 1987; Heimlich-Boran 1988; Ford 1989). Specific behaviour events such as spyhops, lobtails and leaps have generally been described in terms of subjective assessments of their 'meaning' or communicative content (e.g. Pryor 1986; Shane 1990). Some researchers have gone beyond such personal interpretations by correlating specific leap types with surface feeding (Würsig and Würsig 1979), behaviours with sounds (e.g. Clark 1982), or sexual behaviours with hormone levels (Wells 1986). Sequence analysis has been used to study cetacean sounds (Ford 1989), but, surprisingly, not to classify their behaviour.

Behaviour sequence analysis is a quantitative and repeatable method of describing association patterns between behaviour events and classifying behaviours (e.g. Bakeman and Gottman 1986 and references therein). Associations between behaviours help answer the question of what makes a dolphin use a given behaviour pattern. In addition, the resulting behaviour categories can be correlated with other factors such as group size and composition. Here, I extend the use of behaviour sequence analysis to marine mammal behaviour.

My first aim was to classify Hector's dolphin behaviours on the basis of the sequences in which they use them. The second aim was to complement studies of reproduction and population biology of Hector's dolphin (Chapters 1-5) by investigating the social context in which sexual behaviours occur.

Methods

Behavioural observations

Hector's dolphins were observed off Banks Peninsula (east coast of South Island, New Zealand; 43° 50'S, 172° 56'E) during a three year period (Oct 1985 - Oct 1988). Behavioural observations were made from a 3.9m inflatable boat, which was either stationary or moving at its slowest speed of approximately 1 knot.

Most of the 25 mutually exclusive behaviour events I recorded (Table 1) appeared to reveal motivational state. I also recorded behaviours such as catching fish, copulations, biting and playing with seaweed, and used these to label the behaviour categories which emerged. I excluded from the analysis any behaviour that was very rare, or so difficult to observe it could not be reliably recorded.

Like Altmann (1965) and Gordon (1986, 1988), I recorded each behaviour event in the focal group irrespective of which individual in the group performed it. I defined a 'group' as two or more dolphins in close contact, less than 20 metres from each other and closer to each other than to individuals belonging to other groups (as in Chapter 6). The 'focal group' was typically the group closest to the boat.

Whenever one of the individuals in the focal group performed one of the 25 behaviour events (Table 1), the time and behaviour code were dictated into a small tape-recorder. Tapes were transcribed daily into a computer spreadsheet ("Excel", on a Macintosh computer). Included in the data file were date, location, focal group size, group composition and weather conditions. Only observations made in weather conditions of Beaufort 2 or calmer were used for behaviour sequence analysis.

Table 1. The 25 behaviour events analyzed.

BA BELLY AWAY: One dolphin turning its ventral surface away from another, by swimming on its side next to the other individual and within two body lengths (see BP, SS and UD).
BB BUBBLEBLOW: Dolphin exhales while underwater.
BC BODY CONTACT: Any form of body contact other than pounce (PN), usually not forceful.
BI BITE: One dolphin bites another.
BP BELLY PRESENT: One dolphin turning its ventral surface towards another. Done by swimming on its side next to, or upside-down under the other individual, and within two body lengths (see BA, SS and UD).
CH CHASING: Dolphin swimming at speed following another individual. Mostly this appears to be one dolphin chasing another, but at times they both appear to be chasing something else (fish or another dolphin).
CO CHIN-OUT: Dolphin standing vertical in water with tip of snout out of the water no further than the eyes (see SP).
CP COPULATION: Ventral contact between two dolphins, intromission observed (see PC).
FE FEEDING: Eating or chasing fish.
HF HORIZONTAL FLEX: Dolphin lies at water surface and flexes its body, sometimes accompanied by side-to-side head movements.
HJ HORIZONTAL JUMP: Dolphin leaves water and maintains a horizontal position until re-entering the water snout first (see NJ and VJ).
LO LOBTAIL: Tail is raised above water surface and slapped flat on the water surface in a deliberate and usually forceful movement (see UL).
PC POSSIBLE COPULATION: Ventral contact between two dolphins, no intromission observed (see CP).
PN POUNCE: Forceful body contact involving one dolphin thrusting its ventral surface against the side or dorsal surface of another dolphin (see BC).
PO PENIS OUT: Male showing penis outside genital slit.
NJ NOISY JUMP: Jump which ends in dolphin forcefully slapping part of its body (usually the throat or the side of the head or body) against the water surface (see HJ and VJ).
SP SPYHOP: Dolphin standing vertical in water with head out of the water well past the eyes, usually down to pectoral fins or further (see CO).
SS SWIMMING ON SIDE: Dolphin swimming on its side. Further than two body-lengths from another dolphin (see BA and BP).
TB TOP OF BODY OUT: Front half of body is brought out of water and slides back into water, often done in close contact with other dolphins in an apparent avoidance context.
TO TAIL OUT: Tail lifted out of water and moved back underwater without lobtailing or splashing (see LO, TS and UL).
TS TAILSPLASH: Tail movement at or just under water surface resulting in splash. Tail is not lifted out of the water (see LO, TO and UL).
UD UPSIDE-DOWN SWIMMING: Dolphin swimming upside-down. Further than two body-lengths from another dolphin (see BA and BP).
UL UPSIDE-DOWN LOBTAIL: Lobtail (LO) while swimming upside down.
VJ VERTICAL JUMP: Dolphin jumps out of the water facing directly upwards, and re-enters the water snout-first with the body again in a vertical position (see HJ and NJ).
WE PLAY WITH WEED: Piece of weed is picked up on the snout, pectoral fins or tail.

Behaviour classification

I wrote a "macro" program to inspect each behaviour in turn and score which behaviours followed it within one minute or two minutes (2,651 and 8,904 behaviour transitions, respectively). In other words, if behaviour A was followed by behaviour B (15s after A), followed by behaviour C (20s after A) and then followed by behaviour B again (30s after A), this was scored as A-B (A followed by B) + A-C + A-B + B-C + C-B. I did not score or analyse occurrences of a behaviour following itself, i.e. B-B is not included, as I was interested in the relationship of each behaviour to each other behaviour for the purpose of classifying behaviours. This was taken into account in the calculation of the z-score (see below). In this paper the term 'behaviour transition' is used to mean a 'preceding-following' relationship of two behaviours, for example the behaviour transition LO-VJ is a sequence where VJ follows LO within a specified time period (see Table 1 for behaviour codes).

Z-scores were calculated by dividing the difference between observed and expected frequency by their standard deviation (Bakeman and Gottman 1986). The z-score generated approximates a normal distribution (Bakeman and Gottman 1986) and can be used to determine if particular behaviour transitions occur significantly more often or less often than expected by chance. In this study z-scores are used as an index of the strength of the sequential dependence of two behaviours.

I used the following formula to calculate z-scores (Gottman 1980; Allison and Liker 1982; Bakeman and Gottman 1986):

$$z = \frac{p(t/g) - p(t)}{\sqrt{\frac{p(t)[1 - p(t)][1 - p(g)]}{Np(g)}}}$$

where, *p(t/g)* stands for the observed 'conditional' probability of the target (or following) behaviour *t* occurring after *g*, the given (or preceding) behaviour. *p(t/g)* equals *f(g,t)* divided by *f(g)*, where *f(g,t)* is the frequency of the behaviour transition from *g* to *t*, and *f(g)* is the overall frequency of the given behaviour.

p(t) is the expected 'unconditional' probability, i.e. what one would expect if the probability of the target behaviour was not influenced by the preceding given

behaviour. *p(t)* is equal to the overall frequency of the target behaviour *f(t)* divided by *n,* the total number of behaviour transitions tallied. In this study, transitions involving a behaviour following itself were not of interest. Hence *p(t)* becomes *f(t)/n-f(g).* Sample sizes were sufficient to compare the observed probability of each behaviour transition with that expected by chance (Siegel scores > 9; Siegel 1956; Bakeman and Gottman 1986).

The z-scores were used to construct sequence diagrams. These diagrams are similar to the Maximum Spanning Tree approach to visualizing behaviour sequences (Morgan et al. 1976). Rather than forcing the data into a tree-shaped diagram like a Maximum Spanning Tree, the sequence diagrams show all behaviour associations with z-scores higher than 2.0 allowing networks of associations to show. The arbitrary cut-off level of 2.0 was chosen because z-scores greater than 1.96 (or smaller than -1.96) are considered statistically significant at the $p<0.05$ level (Bakeman and Gottman 1986). Maximum Spanning Trees and similar visual representations require only one score for each behaviour combination, rather than one value for 'x follows y' and a different value for 'y follows x'. The two z-scores for each behaviour combination were averaged before the sequence diagrams were constructed.

Behaviour context analysis

To study the social context in which sexual behaviours occur, I examined whether sexual behaviours were more common in smaller or larger groups of dolphins, in groups with or without calves (individuals less than a year old), and just after groups joined. A simple computer program scored the sexual behaviour rate for 10-minute periods in which calves were either present or absent throughout and the group size remained within the same category (4 group size categories: 1-5; 6-10; 11-15; 16-20 individuals). The program located 10-minute periods which fulfilled these criteria and then scored the number of sexual behaviours (per dolphin per min) for each period.

I used a Kruskal-Wallis test to assess the effect of group size (4 categories) on sexual behaviour rates. The effect of the presence or absence of calves (2 categories) was tested using a Mann-Whitney U-test. When more than one 10-minute score (for a given group size and calves present or absent combination) was available from the same observation period, one randomly chosen score was used in the analysis.

To determine if sexual behaviour was more or less common after two previously separate groups joined, I scored whether the sexual behaviour rate increased, decreased or stayed the same in paired (consecutive) 10-minute samples from the same observation period, where at least one of the samples contained some sexual behaviour.

Results

Behaviour classification

The sequence diagrams (Figs 1 and 2) revealed five behaviour categories with stronger associations within than between categories. The 'sexual' category included 'copulation', 'possible copulation' and 'penis out'. The 'aggressive' category contained 'bite' (BI), 'chase' (CH) and 'tailsplash' (TS). The 'feeding' behaviours FE, SS, CO and HF were among the most closely associated behaviours, and were negatively associated with most other behaviours. Three different types of leap and two forms of lobtailing were closely associated and were labelled 'aerial behaviours'.

The behaviour 'bubbleblow' (BB) was unusual in that it provided a link between some rather different behaviours. It was the only behaviour which was difficult to place in a category, and belonged to a different category in the two analyses. BB was strongly associated with the aggressive behaviours and also with 'playing with weed' (WE), the only clear-cut play behaviour recorded. However, WE itself had very low or negative associations with all of the aggressive behaviours (z-scores <0.7 in 2 minute transition table and down to -1.6 in the 1 minute transition table). For this reason I did not consider lumping WE with the aggressive behaviours, and have tentatively labelled the pair WE-BB 'play'.

Behaviour context

Behaviour context analyses on 132 10-minute samples revealed that behaviours belonging to the sexual category were most common in groups of 11-15 individuals (Kruskal-Wallis $H = 11.6$, $p = 0.009$, $df = 3$). These groups had a mean sexual behaviour rate (per dolphin) more than double that of groups of 1-5 and 6-10 individuals, and almost 20 times that of groups of 16-20 individuals. The sexual behaviour rate was not significantly influenced by the presence or absence of calves in the group (Mann-Whitney $U = 848$, $p = 0.10$, $df = 1$).

Figure 1. Sequence diagram for 1 minute interval between preceding and following behaviour.

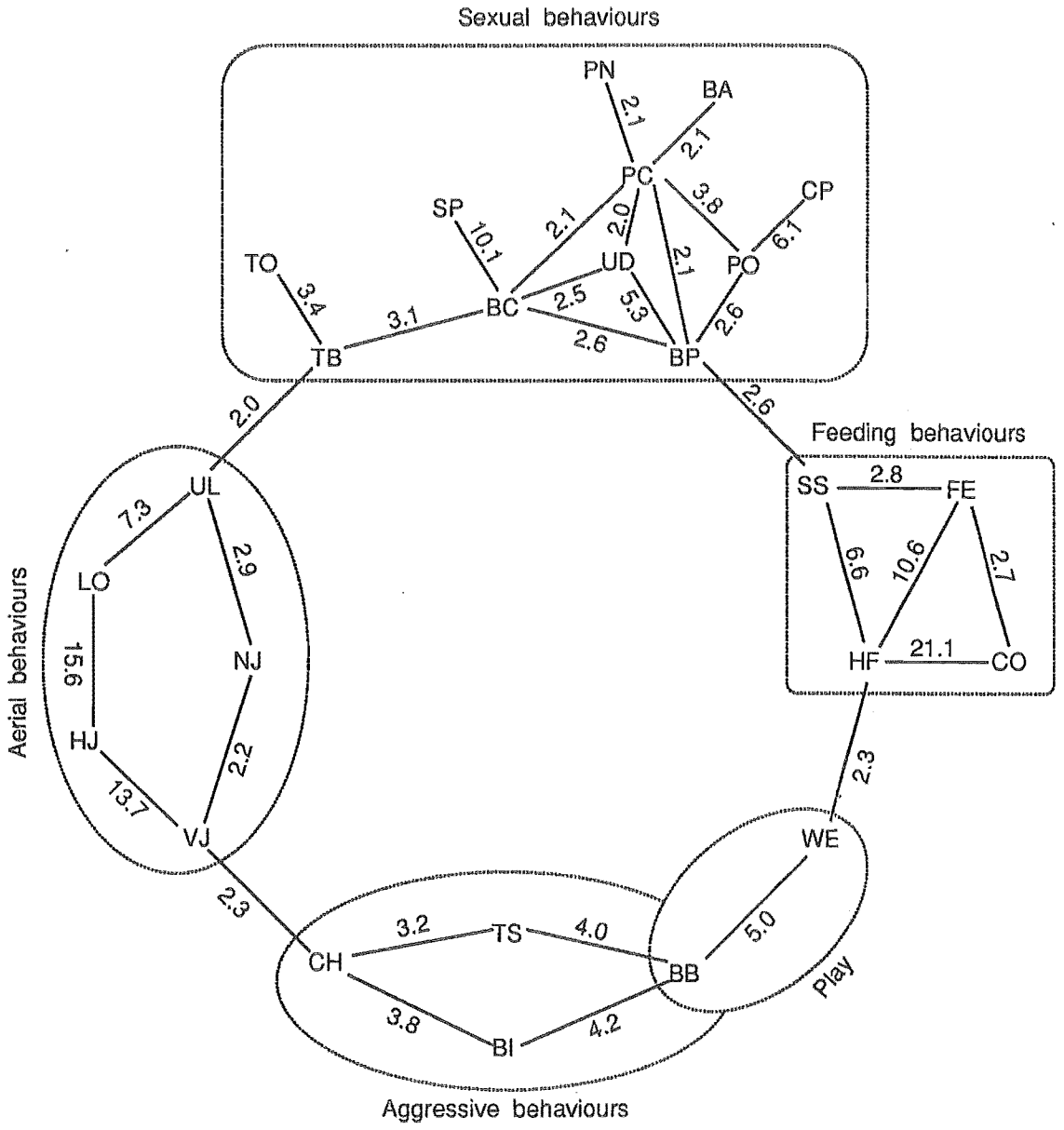
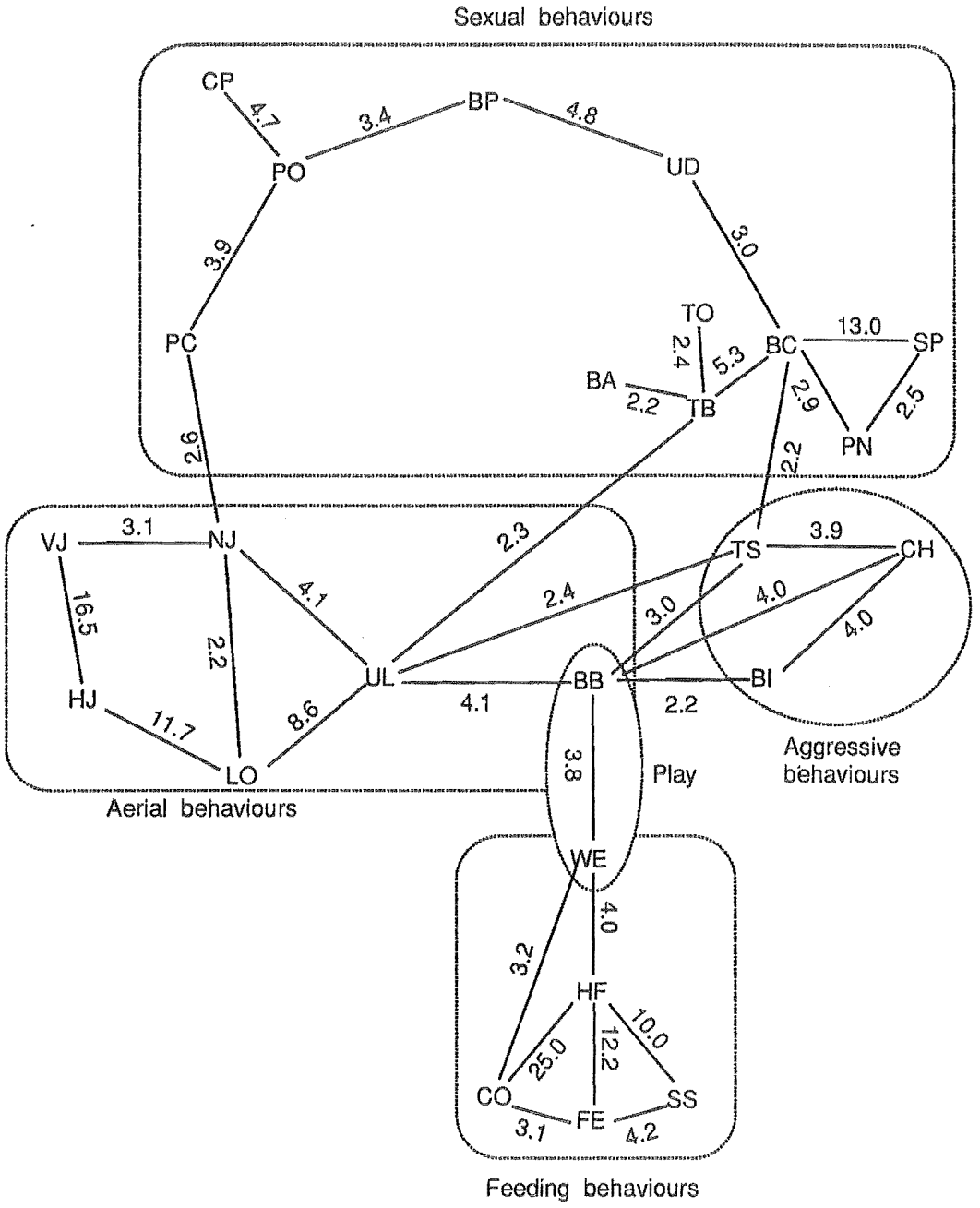


Figure 2. Sequence diagram for 2 minute interval between preceding and following behaviour.



The sexual behaviour rate increased significantly after two or more groups fused. Consecutive pairs of 10-minute samples, at least one of which contained a sexual behaviour were available for 18 group size increases and 49 instances where group size decreased or remained constant. A comparison of the ratio of increases, decreases and no change in the sexual behaviour rate showed almost twice as many increases after groups fused than at other times ($Chi^2 = 7.25$, $p = 0.027$, $df = 2$).

Discussion

Behaviour unfolds as a time sequence of different behavioural events and states, whether one is observing a single individual or a group. In the case of a lone individual, behaviour is likely to be influenced by internal motivational factors such as hunger and hormone levels as well as external factors such as weather conditions and food distribution. In pairs and groups, additional factors become important, as the behaviour of each individual may be influenced also by the social context and by preceding behaviour of the other(s) (e.g. Slater 1973; Morgan et al. 1976; Sacket 1979; Bakeman and Gottman 1986 and references therein; Waas 1988).

In this study, the sequential structure of Hector's dolphin behaviour was used as the basis for a classification of behaviour events. A striking feature of the sequence diagrams was that behaviour categories tended to be linked with two other behaviour categories forming a relatively simple circle-shaped network. The behaviour categories were arranged slightly differently in Figs 1 and 2, but the same basic pattern was evident. The categories were explanatory and relatively easy to interpret.

The 'feeding' behaviours were very closely associated with each other and negatively associated with most other behaviours. 'Bite' was closely associated with other apparently aggressive behaviours like 'tailsplash' and 'chase'. Copulations and 'possible copulations' were associated with other behaviours one might have intuitively classified as sexual or social such as 'belly present', 'penis out' and 'body contact'.

The aerial behaviours were most strongly associated with sexual and aggressive behaviours. This association, and the high activity level of aerial

behaviours suggests that they are indicative of a high level of excitement, which can be aggressive or sexual excitement depending on the situation. The leaps especially give the strong impression of being used in play. Both leaps and lobtails are highly visible and audible, and are likely to be used as social signals (Norris and Dohl 1980; Saayman and Tayler 1979; Würsig and Würsig 1980). Dawson (1990) found that the aerial behaviours were strongly associated with high pulse-rate sounds, in which the repetition rate of ultrasonic clicks is audible as a "cry", and argued that these sounds are indicative of a high motivational state.

Some researchers have suggested that lobtailing (LO and UL) indicates annoyance or aggression, while others do not agree (see Pryor's 1986 review). In Hector's dolphin behaviour, lobtails were strongly associated with leaps, and outside the aerial category with bubbleblowing, aggressive and sexual behaviours. It appears that in Hector's dolphins, and perhaps in other cetaceans also, lobtailing indicates excitement and sometimes, but not always, annoyance.

The same interpretation applies to bubbleblowing (BB), which has been argued to indicate surprise and possibly aggression (Pryor 1986). The sequence analysis suggests that in Hector's dolphins bubbleblowing is most strongly associated with play, aggression and aerial behaviours in that order. Bubbleblowing appears to indicate a high level of excitement which can be used in aggressive, playful or sexual contexts. These 'excitement' behaviours may be analogous to human shouting, i.e. a behaviour which adds emphasis but the precise meaning of which depends on the context.

The forcefulness of the 'pounce' behaviour suggests it is an aggressive behaviour, but the fact that the 'pouncer' hits the other individual with the belly suggests a more sexual behaviour or a dominance/sexual connotation. The sequence analysis shows it has stronger links with sexual than aggressive behaviours. Pounce (PN) is included in the category of sexual behaviours, and at the 1 minute level is most closely associated with possible copulation (PC), while at the 2 minute level it is most closely associated with body contact (BC) which in turn is most closely associated with the aggressive category. A pounce may be analogous to a 'dominance mounting'. Östman (In press) found that sexual contacts between captive male bottlenose dolphins correlated with changes in their dominance relationship and their interactions

with females. It is possible that some of the behaviours in the 'sexual' category are used in competitive interactions between males or females. However, obviously aggressive behaviours such as biting were relatively rare and never associated with sexual behaviour.

Most of the behaviour events quantified in this study have been observed in many other species of dolphins, porpoises and whales. Behaviour sequence work carried out on these other species may justify the often intuitive groupings of behaviours used to define broad activity patterns such as foraging, travelling, milling and resting (e.g. Heimlich-Boran 1988; Ford 1989; Shane 1990).

The analyses of behaviour sequences and behaviour context provide an insight into the interactions within groups of Hector's dolphins and the social structure of groups. Sexual behaviour rates were higher in relatively large groups and after previously separate groups came together. This suggests that the definition of 'group' used in this study had meaning to the dolphins themselves, as they changed their behaviour when two or more groups came together. Studies of other dolphin species have also suggested that social and apparently sexual behaviour is more common when previously separate groups or individuals meet (e.g. Saayman and Tayler 1979; Würsig and Würsig 1979).

The social interactions within and between groups are of obvious conservation significance, particularly for an animal like Hector's dolphin which has a small total population size (Dawson and Slooten 1988), and has suffered high entanglement rates in inshore gillnets (Dawson 1990). A reduction in absolute numbers will tend to make finding appropriate mates more difficult, as fewer will be available. The typically clumped nature of Hector's dolphin distribution suggests that in some areas individuals would need to travel large distances if they could not find a mate in their local group. The behaviour analysis presented here suggests a subtler effect also. The fusion of groups appears to be important in stimulating sexual behaviour. It seems possible that sexual behaviour rates are lower where groups are widely separated, and that this could be reflected in lower pregnancy rates in low density areas.

Both group composition (Chapter 6) and behavioural data suggest that Hector's dolphins live in flexible 'fission-fusion' societies. Males do not appear

to monopolize females or groups of females for mating, and their small size compared to the females may mean this is not a feasible option (Chapter 3). Behavioural information, as well as the males' small body size and large testis size, point towards a promiscuous mating system in which males search for rather than monopolize sexually active females (see Chapter 3 and thesis Discussion). This hypothesis is also supported by the absence of strong associations between aggressive and sexual behaviours in the behaviour sequence analysis.

Mating systems can not necessarily be inferred directly from social organization or sexual dimorphism (Rowell 1979; Rowell and Chism 1986), and this discussion is certainly not meant as the last word on Hector's dolphin mating behaviour. However, a promiscuous mating system in which males search for rather than monopolize females appears to be most likely, therefore I have explored the conservation implications of such a mating system (see Chapter 3 and thesis Discussion).

Discussion

To improve our knowledge of the conservation biology of Hector's dolphin, I have integrated studies of age, reproduction, survival, population growth and behaviour. Before this study, little was known about the population biology and behaviour of this species (Baker 1978, 1984). Their small population size and limited distribution (Dawson and Slooten 1988) suggested that Hector's dolphins might be vulnerable to human impact, such as entanglement in gillnets (Baker 1978, 1984). Interviews with commercial and amateur fishers in the Pegasus Bay-Canterbury Bight area (Dawson 1990) confirmed earlier suspicions of high levels of gillnet entanglement (Cawthorn 1988). This study has provided data on the population biology and social organization of Hector's dolphins that were needed to assess human impacts on their populations.

Population biology

Combining data on age and reproduction showed that Hector's dolphins have a relatively low reproductive rate, similar to those of other small dolphins and porpoises (e.g. Gaskin et al. 1984; Perrin and Reilly 1984). Females give birth to their first calf at 7 to 9 years old, and thereafter have one calf every 2 to 3 years. This means that a female reaching maximum age (around 19 years) could produce a maximum of four to seven calves.

Population models based on these reproductive parameters predicted maximum population growth rates of 1.8 to 4.4% per year. The population models were also used to explore the likely consequences of management strategies which reduce entanglement mortality. Population size and population growth rates may fluctuate markedly for several decades after a significant reduction in entanglement mortality, especially if the age structure of the population is biased towards younger individuals. These results emphasize the importance of long-term population monitoring before concluding whether conservation management has been successful or not.

Cetaceans have the relatively low reproductive rates and high parental investment typical of the larger mammals (Goodman 1981). The life-histories of cetaceans are characterized by single births after a relatively long gestation,

and by relatively great longevity, slow maturation, and late weaning (Perrin et al. 1984).

Within the Delphinidae (the family to which Hector's dolphin belongs), sexual maturity is reached at around 6-12 years old (Perrin and Reilly 1984; Reilly and Barlow 1986). The minimum calving interval is 2-4 years, although much longer calving intervals have been reported (Perrin and Reilly 1984; Kasuya and Marsh 1984; Reilly and Barlow 1986). Longevity varies widely, from an estimated 18 years for Commerson's dolphin *Cephalorhynchus commersonii* (Lockyer et al. 1988a) to at least 63 years for pilot whales *Globicephala macrorhynchus* (Kasuya and Marsh 1984) and probably longer for orca *Orcinus orca* (Bigg 1982).

With roughly the same age at first maturity and minimum calving interval, those delphinids with a relatively long life-span should have a greater potential for population increase. Maximum population growth rates of up to 9% per year are thought to be possible for dolphin species with a maximum age of 50 years, given an average calving interval of 2 years and an annual non-calf survival rate higher than 0.96 (Reilly and Barlow 1986). Commerson's dolphin *Cephalorhynchus commersonii* and Hector's dolphin *C. hectori*, with longevities of 18 and 20 years respectively, are among the shortest-lived delphinids, and are therefore expected to have low population growth rates (cf. Barlow 1986).

Of course, the highest population growth rates calculated in population models are often not achieved in wild populations (Reilly and Barlow 1986). Pilot whales and other longer-lived delphinids appear to have longer calving intervals and a lengthy post-reproductive phase (Kasuya and Marsh 1984). In a study of 373 female pilot whales stranded or killed in Japanese "small type whaling" or drive fisheries, Kasuya and Marsh (1984) found that females matured at age 7-12 and lived to 63 years, but produced an average of only four to five calves in a lifetime and had their last calf before age 40.

A further caveat is required in applying population growth rate estimates from mathematical models to management situations. Management schemes that incorporate the concept of net production (sustainable yield available for harvest, or population growth increment) are based on the assumption that reproductive rates and/or natural mortality rates change in a compensatory

way with population density (Perrin and Donovan 1984; Perrin and Reilly 1984; Smith 1983). Unfortunately, the reproductive rates of whales and dolphins do not necessarily increase with decreasing population size (Mizroch 1983; Mizroch and York 1984; Perrin and Reilly 1984). With their relatively low reproductive rates, and apparent lack of density dependent population growth, dolphins are extremely vulnerable to human impacts on their populations.

Social organization and behaviour

The social organization of Hector's dolphins is of interest in its own right, and also has implications for conservation management (see below). Working closely with another biologist, Steve Dawson, I used photographic identification to study the association patterns among Banks Peninsula Hector's dolphins. Associations were relatively fluid, both males and females associating loosely with a relatively large number of other individuals (males more so than females), rather than having a few very close associates.

In cetaceans, as in land mammals (e.g. Rubenstein and Wrangham 1986), group size and structure are influenced by a network of factors, including habitat, social interactions, and the requirements of feeding, avoiding predation, finding mates, and caring for young (Wells et al. 1980; Norris and Schilt 1988; Shane et al. 1986; Würsig 1989). Within this network, group size and distribution affect social and sexual interactions, and vice versa (e.g. Rubenstein and Wrangham 1986).

Group size varies widely among cetaceans. Baleen whales are generally found alone or in small groups (e.g. Gaskin 1982; Evans 1987). Toothed whales are more strongly gregarious with most feeding, social activity, mating and rearing of young taking place within the context of a group of individuals (e.g. Würsig 1989). Among the toothed whales, group size appears to correlate with habitat structure and activity patterns. Groups tend to be larger in relatively deep and open water. Near-shore toothed whales usually occur in groups of a dozen or so individuals, while offshore species tend to form larger groups, of up to hundreds or even thousands of individuals (e.g. Wells et al. 1980; Shane et al. 1986; Würsig 1989).

Inshore delphinids generally live in small groups of no more than a few dozen individuals, and group structure ranges from very stable in orca (Balcomb et

al. 1982; Bigg 1982) to very fluid in most dolphins (Würsig 1989). Orca resident off British Columbia and Washington State live in remarkably stable groups, which, except for births and deaths, have remained unchanged for the 20 years they have been studied (Balcomb et al. 1982; Bigg 1982). Dolphins generally live in much more open groups which often exchange members with groups that have adjacent or overlapping ranges (Wells et al. 1987; Würsig and Würsig 1979; Saayman and Tayler 1979; Scott et al. 1990).

Different populations of the same species may have a different characteristic group size, and indeed the same individuals may occur in large or small groups depending on sexual maturity, group activity and habitat. For example, bottlenose dolphins *(Tursiops truncatus)* tend to form larger groups in deep-water passes and in the offshore Gulf of Mexico than in the shallow inshore waters of Florida (Wells 1986). Variations in group size with underwater geography are thought to be related to foraging techniques and the need for protection from predation (Shane et al. 1986). Shallow, inshore waters may provide relatively predictable and evenly distributed food resources associated with reefs or sea-grass flats, while schooling pelagic fish and squid are the predominant prey in more open waters (Shane et al. 1986). Larger groups of dolphins may be better at locating these patchy but rich food sources offshore, and may provide the numbers of individuals necessary to cooperatively herd the prey. In addition, large groups could have advantages for predator avoidance (Shane et al. 1986).

Rapid changes in dolphin group size may coincide with changes in environment and feeding behaviour. For example, dusky dolphins *(Lagenorhynchus obscurus)* off Argentina search for fish schools in many spread-out, small groups of dolphins. Once prey are found, the dolphin groups aggregate, feed cooperatively, socialize in these large aggregations, and then split up again (Würsig and Würsig 1980). This relatively fluid social structure has been labelled a fission-fusion society (e.g. Würsig 1989), and has been compared with ungulates (e.g. Wells et al. 1980), as well as chimpanzees and baboons (e.g. Tayler and Saayman 1972; Saayman and Tayler 1979; Wells et al. 1980).

Spinner dolphins *Stenella longirostris* appear to have the most loosely structured social organization among the studied delphinids. Spinner dolphins are primarily pelagic and, unlike inshore dolphins, often occur in large groups

of hundreds or thousands of individuals (Norris and Dohl 1980; Norris et al. 1985; Leatherwood at al. 1988). Their groups appear to be highly dynamic assemblages of variable size and composition, with only small subgroups remaining stable for any length of time (Norris and Dohl 1980; Norris et al. 1985).

Within the range of known delphinid social systems, Hector's dolphins appear to be most similar to bottlenose dolphins. Group size and composition are not quite as fluid as in spinner dolphins (Norris and Dohl 1980; Norris et al. 1985), and certainly not as stable as in orca (Balcomb et al. 1982; Bigg 1982). Both bottlenose dolphins (Wells et al. 1987) and Hector's dolphins appear to be resident in relatively small geographical areas, forming relatively closed populations. Within a population, however, each individual associates loosely with a relatively large number of other individuals, rather than having a few very close associates. In both species, small groups of regularly recurring associates appear to travel through their range frequently joining other groups for periods of minutes or hours.

To gather more detailed information on the social interactions of Hector's dolphins, I studied their social and sexual behaviour. Behavioural studies of cetaceans have tended to focus on broad categories of activity such as foraging, travelling, milling, resting and so on (e.g. Würsig and Würsig 1979, 1980; Heimlich-Boran 1988). Where specific behaviour events (e.g. leaps, body contacts) have been studied, they have often been described and categorized in terms of the researcher's subjective impression of their 'meaning' or communicative content (e.g. Pryor 1986; Shane 1990).

I have tried to take a step beyond this approach, by recording behavioural events rather than categories, and by using behaviour sequence analysis to categorize behaviours in a quantitative and repeatable way (e.g. Bakeman and Gottman 1986). Behaviour unfolds as a sequence, in which each behaviour is influenced by the behaviours that went before. By categorizing behaviours on the basis of these sequences I have attempted to reflect as closely as possible how the dolphins themselves interpret their behaviours.

Hector's dolphin behaviours were classified into five categories - 'feeding', 'sexual', 'aggressive', 'play' and 'aerial'. In order to complement the studies of reproduction and population biology, I investigated the social context in which

Hector's dolphins use sexual behaviours. The number of sexual behaviours per individual was highest in groups of 11-15 dolphins, and tended to increase after groups came together.

The fluid association patterns and increase in sexual behaviours after groups come together suggest that Hector's dolphins have a promiscuous mating system. Hector's dolphins have very large testes for their body size, and males appear to increase their chances of fertilizing females by searching for sexually active females rather than attempting to monopolize them.

Very little is known about reproductive behaviour and mating systems of cetaceans. In many whales, dolphins and porpoises, copulation appears to be important socially as well as reproductively (e.g. Würsig 1989; Brownell and Ralls 1986). Cetacean mating systems have been the subject of much speculation. Brownell and Ralls (1986) discussed mating systems in baleen whales and suggested that mate monopolization is more common in species with relatively small testes. They argued that in baleen whale species with relatively small testes, males may compete primarily by monopolizing females and preventing other males from copulating with them. In these species females are thought to copulate with one or a small number of males each season, and interactions between males are often highly aggressive. Baleen whales with relatively large testes (e.g. right whales), are thought to have promiscuous mating systems in which male-male interactions are not highly aggressive (Brownell and Ralls 1986).

Relatively large testis size, fluidity of individual associations, and observations that females mate with more than one male, suggest that most dolphins have polygynous or promiscuous mating systems (Wells et al. 1987; Würsig 1989). Hector's dolphins fall within these generalizations. They live in relatively open groups of two to eight individuals, which, in areas of high abundance, frequently come together and exchange members. As in bottlenose dolphins (Wells et al. 1987), there was no evidence that male Hector's dolphins monopolize females, or that pair bonds are formed.

Conservation

Conservation science aims to identify conservation threats and to study populations for their susceptibility to these threats or risks (e.g. Gilpin and Soulé 1986; Gough 1988; Mace and Ballou 1990). While genetic problems may threaten a species in the final stages of extinction (Gilpin and Soulé 1986), the most immediate conservation risks tend to be associated with population biology (Lande 1988; Mace and Ballou 1990). Besides reproductive biology and survival rates, social factors can play a major role in extinction events (e.g. Gilpin and Soulé 1986; Lande 1988; Simberloff 1988). In small or fragmented populations it may be more difficult for individuals to find mates or to form social groups necessary for successful reproduction, feeding or defense from predators (e.g. Allee et al. 1949; Soulé 1983; Simberloff 1988).

The relatively low population growth rates reported in this thesis are a major cause for concern, considering the small total population of 3000-4000 Hector's dolphins (Dawson and Slooten 1988) and the human impacts on it (Dawson 1990). Interviews with commercial and amateur fishers in the Pegasus Bay-Canterbury Bight area (Dawson 1990) revealed catch levels which exceeded even the most optimistic population growth rate estimates for the local population. In this area, at least 230 dolphins were reported killed in gillnets between 1984 and 1988 (Dawson 1990), an average of 57.5 per year. The local population, estimated at about 740 individuals in 1984-85 (Dawson and Slooten 1988), would be expected to increase by a maximum of 13.3 to 32.6 individuals per year (1.8 to 4.4% population growth rate).

I should stress that the maximum population growth rate represents the potential for population growth under ideal conditions (see Chapter 4; Reilly and Barlow 1986; Barlow and Boveng In press). For example, to achieve the 4.4% population growth rate, annual survival rates were assumed to average 0.95 from birth, with the only added risk of mortality to juveniles in the first year of life coming from the death of the mother. Survival rates based on human data (Barlow and Boveng In press), in combination with the most optimistic reproductive rates, resulted in a maximum population growth rate for Hector's dolphins of 4.1%. Barlow and Boveng emphasize that this represents an absolute limit to the likely survivorship of any wild population of marine mammals. The next most optimistic survival rate curve, resulted in a

population growth rate of 1.8% for Hector's dolphins, and represents a more plausible "best case" scenario.

A second indication that the Pegasus Bay-Canterbury Bight population was unable to cope with recent gillnet entanglement levels came from survival rates observed in this population. Survival rates (including gillnet mortality) were estimated from a photographic identification study. Population models using these survival rates, even in combination with the most optimistic reproductive rates, consistently resulted in a decreasing population.

Studies of Hector's dolphin behaviour point to other potential conservation risks. As Hector's dolphins become rarer, facets of their social organization and behaviour may exacerbate population decline. The fusion of groups appears to be important in stimulating sexual behaviour, and males appear to increase their chances of reproduction by increasing the number of encounters with sexually active females, rather than by monopolizing females. If males travel from one group of females to another, searching for sexually active females, there are more likely to be times when a fertile female is not accompanied by a mature male and not inseminated. This form of mate searching behaviour is likely to result in relatively high fertilization rates in areas where Hector's dolphins are common, but could depress fertilization rates in low density areas (Whitehead 1987; Whitehead and Arnbom 1987). This could lead to a downwards spiral with a decrease in population size leading to a lower reproductive rate, which further decreases the population size and so on (e.g. Gilpin and Soulé 1986).

Males may change their mate searching behaviour as the distance and travel time between groups increases. However, there are several reasons why this may not necessarily solve the problem. Firstly, female fertilization rates may be lowered well before travel times become unacceptable to males. Secondly, male and female distributions and mate searching behaviours may be constrained by other factors such as the distribution of food and predators. Thirdly, searching for sexually active females by moving from group to group may be the only option open to male Hector's dolphins. They may never change to a polygynous or monogamous mating system if the males (which are smaller than females) are incapable of preventing individual females, let alone groups of them, from mating with other males.

Thus, while population growth rate calculations indicate whether an existing population can cope with a given impact, data on social behaviour can help predict whether a decrease (or increase) in population size is likely to affect behaviour and reproduction. Besides identifying potential conservation risks, a thorough understanding of the biology and behaviour of a species can help interpret the results of population survey data. A population's response or lack of response to conservation measures can be fully understood only with sufficient knowledge of reproductive behaviour as well as reproductive biology.

Other potentially important impacts or risks, which have not been specifically addressed in this study, include pollution, disease and overfishing. Significant levels of DDT (total DDT ranging from 1.96 to 52.85 ppm), PCBs (total PCB 0.95 to 10.21 ppm) and Dioxin (total TCDD TE 11 to 37 ppt) have been found in the tissues of Hector's dolphins (Buckland et al. 1990; Slooten and Dawson unpub. data). These compounds are known to interfere with reproduction (Helle et al. 1976a, b; Bowman et al. 1989), and their effects are worsened by synergism between compounds (Reijnders 1989). It is not known to what extent pesticide contamination or other forms of pollution contribute to mortality or to the low reproductive rates observed in Hector's dolphins. Likewise, it would be very difficult to determine to what extent pollution, overfishing and habitat degradation have affected inshore fish stocks, and thereby the feeding and movement patterns of Hector's dolphins.

Events like catastrophic pollution and disease are even more difficult to predict. While ship traffic around New Zealand is relatively light compared with more industrialized parts of the world, a major spill of oil or some other contaminant is certainly a possibility. Epidemics, such as the phocid distemper virus which killed seals and other marine mammals in the eastern Atlantic (Pearce 1988), are similarly sudden and unpredictable. These unpredictable events underscore the risks of impacting a population to the point where it is unable to grow.

Future research

The Department of Conservation has begun a series of aerial surveys to monitor population size in the Pegasus Bay-Canterbury Bight area. Population surveys covering the entire distribution of Hector's dolphins would be highly

desirable. These could take the form of a repeat of our 1984-85 boat survey (Dawson and Slooten 1988), or a series of aerial surveys which have the advantage of being faster and therefore easier to replicate.

Further information on gillnet entanglement levels in the Pegasus Bay-Canterbury Bight area and elsewhere will need to come from active investigations by DOC, MAF, or both. Although they are legally required to do so, commercial and amateur fishers have traditionally been reluctant to report incidental catches of marine mammals, fearing that this would lead to more restrictive fishing regulations (Cawthorn 1988). The establishment of the Banks Peninsula Marine Mammal Sanctuary, demonstrating a direct link between the reporting of marine mammal deaths and fishing restrictions, has almost certainly increased this reluctance.

One possible method of studying entanglement rates would be to place observers on fishing vessels, and at land observation posts in areas where gillnetting takes place close to shore. Another, complementary method of estimating catch per unit effort would be to conduct gillnetting trials from a research vessel or chartered fishing vessel. In this case the researcher could determine the places and times in which nets are used, and compare entanglement rates between day and night sets, different gillnetting techniques and areas of different dolphin abundance, for example. A third approach would be to pay a retrieval fee to fishers who bring in dead dolphins they have found in their nets (see Read and Gaskin 1988). If the same fishers provided accurate effort statistics, this would provide another estimate of the number of dolphins caught per unit effort. A retrieval fee system is unlikely to work in New Zealand, since the link between the reporting of marine mammal deaths and fishing restrictions has received widespread publicity.

Continued dissections of dead Hector's dolphins, retrieved from gillnets or found on beaches, would provide important data on reproductive rates, survival rates and age structure. These data would allow more precise population modelling, and would facilitate studies of the effectiveness of the sanctuary. Tissue samples from these dead animals could also be tested for contamination by pollutants and could be used for genetic work. Studies revealing the amount of genetic interchange between Hector's dolphin populations in different areas, could help determine the geographic scale of

human impacts. Unfortunately, detailed dissections appear to have stopped at the end of this study.

Continued photographic identification work in the Pegasus Bay-Canterbury Bight area is aimed at improving estimates of survival and calving rates. Photographic identification surveys to the north and south of Banks Peninsula will provide further information about movements of individuals. These movement data will be important in assessing how many of the individuals which disappear from the photographic catalogue have died and how many have emigrated.

An area inhabited by a small population of Hector's dolphins, a few dozen rather than several hundred individuals, would be best suited to more detailed observations of association patterns and behaviour. A smaller population would allow the use of subtler markings to identify individual dolphins, and would improve one's chances of encountering a particular individual. This would be especially advantageous for studies of calf survival as younger individuals have not had time to accumulate the more obvious fin nicks and body scars. Likewise, focal animal observations of behaviour would be much easier in a smaller population. Comparative data on behaviour and calving interval from areas of relatively high and relatively low Hector's dolphin abundance would help determine the extent to which population density affects social organization and fertilization rates.

In Conclusion

Hector's dolphin is now far better known, in terms of its conservation biology, than the other three species in the genus *Cephalorhynchus*. This thesis provides data on population biology and social organization of Hector's dolphins which are necessary for assessing the impact of gillnetting mortality on the population, and for identifying additional conservation risks. Maximum population growth rates of Hector's dolphins were low (1.8-4.4% per year), and were exceeded by recent gillnet entanglement rates in the Pegasus Bay-Canterbury Bight area. Reproductive rates of whales and dolphins do not necessarily show a compensatory increase with decreasing population size (Mizroch and York 1984; Perrin and Reilly 1984). Furthermore, studies of the social organization and behaviour of Hector's dolphins suggested that, once

started, a population decline could be aggravated as fertilization rates may decrease with a decrease in population density.

In recent years, gillnet entanglement has clearly been a serious problem off the Canterbury coast, and possibly also in other areas where intensive gillnetting overlaps with the distribution of Hector's dolphins. Population models using survival rate estimates from the Banks Peninsula population (including gillnet mortality) resulted in a decreasing population, even in combination with the most optimistic reproductive rates. As there are other potential risks to Hector's dolphin populations, including pollution, overfishing and disease, it would be irresponsible to allow gillnetting mortality to approach the level of population growth rates.

Fortunately, gillnet entanglement is easily avoided, compared to the other risks to Hector's dolphin populations, by banning or restricting the use of gillnets in areas where Hector's dolphins are common. After an intensive period of consultation with scientists, the Ministry of Agriculture and Fisheries and the public, the Department of Conservation has created a marine mammal sanctuary around Banks Peninsula with the aim of reducing the level of gillnet entanglement.

New and continued research will improve available data on population size, population trends, survival and reproductive rates. These data will enhance our knowledge of the conservation biology of Hector's dolphins and will help assess the effectiveness of the Banks Peninsula Marine Mammal Sanctuary.

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References

Allee, W.C., Emerson, A.E., Park, O., Park, T. and Schmidt, K.P. 1949. Principles of animal ecology. Saunders, Philadelphia.

Allison, P.D. and Liker, J.K. 1982. Analyzing sequential categorical data on dyadic interaction: A comment on Gottman. Psych. Bull. 91: 393-403.

Altman, P.L. and Dittmer, D.S. (Eds). 1972. Biology data book. Volume I, second edition. Fed. of Am. Societies Exp. Biol., Bethesda.

Altmann, S.A. 1965. Sociobiology of rhesus monkeys. II: Stochastics of social communication. J. Theoret. Biol. 8: 490-522.

Arnbom, T. 1987. Individual identification of sperm whales. Rep. Int. Whal. Commn 37: 201-204.

Bagenal, T.B. (Ed.). 1974. Ageing of fish. Proceedings of an international symposium. Unwin Bros Ltd, England.

Baird, R.W. and Stacey, P.J. 1988. Variation in saddle patch pigmentation in populations of killer whales *(Orcinus orca)* from British Columbia, Alaska, and Washington State. Can. J. Zool. 66: 2582-2585.

Bakeman, R. and Gottman, J.M. 1986. Observing interaction. An introduction to sequential analysis. Cambridge University Press, Cambridge.

Baker, A.N. 1978. The status of Hector's dolphin, *Cephalorhynchus hectori* (van Beneden), in New Zealand waters. Rep. Int. Whal. Commn 28: 331-334.

Baker, A.N. 1984. New Zealand's Hector's dolphin - status at 1984. Paper SC/36/SM23 to the International Whaling Commission Scientific Committee.

Balcomb, K.C., Boran, J.R. and Heimlich, S.L. 1982. Killer whales in greater Puget Sound. Rep. Int. Whal. Commn 32: 681-685.

Barlow, J. 1986. Factors affecting the recovery of *Phocoena sinus,* the vaquita or Gulf of California harbor porpoise. NMFS Admin. Rep. LJ-86-37. Available from Southwest Fisheries Center, P.O. Box 271, La Jolla, CA 92038, U.S.A.

Barlow, J. 1987. An assessment of the status of harbor porpoise populations in central California. NMFS Admin. Rep. LJ-87-06.

Barlow, J. and Boveng, P. In press. Modeling age-specific mortality for marine mammal populations. Mar. Mamm. Sci..

Barlow, J. and Hohn, A. 1984. Interpreting spotted dolphin age distributions. NOAA Technical Memorandum NMFS-SWFC-48.

Bartlett, P.C., Ngategize, P.K., Kaneene, J.B., Kirk, J.H., Anderson, S.M. and Mather, E.C. 1986. Cystic follicular disease in Michigan Holstein-Friesian cattle: Incidence, descriptive epidemiology and economic impact. Preventive Veterinary Medicine 4: 15-33.

Bateson, P.P.G. 1977. Testing an observer's ability to identify individual animals. Anim. Behav. 25: 247-248.

Bekoff, M., Daniels, T.J. and Gittleman, J.L. 1984. Life history patterns and the comparative social ecology of carnivores. Ann. Rev. Ecol. Syst. 15: 191-232.

Benirschke, K., Johnson, M.L. and Benirschke, R.J. 1980. Is ovulation in dolphins, *Stenella longirostris* and *Stenella attenuata*, always copulation-induced? Fish. Bull. 78: 507-528.

Benirschke, K. and Marsh, H. 1984. Anatomic and pathologic observations of female reproductive organs in the short-finned pilot whale, *Globicephala macrorhynchus.* Rep. Int. Whal. Commn, Special Issue 6: 451-455.

Best, P.B. 1967. The sperm whale *(Physeter catodon)* off the west coast of South Africa. 1. Ovarian changes and their significance. Division of Sea Fisheries (South Africa) Investigational Report No. 61.

Best, P.B. 1969. The sperm whale *(Physeter catodon)* off the west coast of South Africa. 3. Reproduction in the male. Division of Sea Fisheries (South Africa) Investigational Report No. 72.

Best, P.B. 1976. Tetracycline marking and the rate of growth layer formation in the teeth of a dolphin *(Lagenorhynchus obscurus).* S. Afr. J. Sci. 72: 216-218.

Bigg, M. 1982. An assessment of killer whale *(Orcinus orca)* stocks off Vancouver Island, British Columbia. Rep. Int. Whal. Commn 32: 655-666.

Bowman, R.E., Schantz, S.L., Weerasinghe, N.C.A., Gross, M.L. and Barsotti, D.A. 1989. Chronic dietary intake of 2,3,7,8-tetrachlorodibenzo-p-dioxin (TCDD) at 5 or 25 parts per trillion in the monkey: TCDD kinetics and dose-effect estimate of reproductive toxicity. Chemosphere 18: 243-252.

Braham, H.W. 1984. Review of reproduction in the white whale, *Delphinapterus leucas,* narwhal, *Monodon monoceros,* and Irrawaddy dolphin, *Orcaella brevirostris,* with comments on stock assessment. Rep. Int. Whal. Commn, Special Issue 6: 81-90.

Brownell, R.L. Jr. 1984. Review of reproduction in platanistid dolphins. Rep. Int. Whal. Commn, Special Issue 6: 149-158.

Brownell, R.L. and Ralls, K. 1986. Potential for sperm competition in baleen whales. Rep. Int. Whal. Commn, Special Issue 8: 97-112.

Brownell, R.L., Ralls, K. and Perrin, W.F. 1989. The plight of the 'forgotten' whales: It's mainly the small cetaceans that are now in peril. Oceanus 32: 5-11.

Buckland, S.J., Hannah, D.J., Taucher, J.A., Slooten, E. and Dawson, S.M. 1990. Polychlorinated dibenzo-p-dioxins and dibenzofurans in New Zealand's Hector's dolphin. Chemosphere 20: 1035-1042.

Buckland, S.T. In press. Estimation of survival rates from sightings of individually identifiable whales. Rep. Int. Whal. Commn, Special Issue 12 (Individual recognition and the estimation of cetacean population parameters).

Cairns, S.J. and Schwager, S.J. 1987. A comparison of association indices. Anim. Behav. 35: 1454-1469.

Caughley, G. 1977. Analysis of vertebrate populations. John Wiley and Sons, Chichester.

Cawthorn, M.W. 1988. Recent observations of Hector's dolphin, *Cephalorhynchus hectori,* in New Zealand. Rep. Int. Whal. Commn, Special Issue 9: 303-314.

Cheverud, J.M., Dow, M.M. and Leutenegger, W. 1985. The quantitative assessment of phylogenetic constraints in comparative analyses: Sexual dimorphism in body weight among primates. Evolution 39: 1335-1351.

Cipriano, F. 1985. Dusky dolphin research at Kaikoura, New Zealand: A progress report. Mauri Ora 12: 151-158.

Clark, C.W. 1982. The acoustic repertoire of the southern right whale, a quantitative analysis. Anim. Behav. 30: 1060-1071.

Collet, A. and Harrison, R.J. 1981. Ovarian characteristics, corpora lutea and corpora albicantia in *Delphinus delphis* stranded on the Atlantic coast of France. Aquat. Mamm. 8: 69-76.

Collet, A. and Robineau, D. 1988. Data on the genital tract and reproduction in Commerson's dolphin, *Cephalorhynchus commersonii* (Lacépède, 1804), from the Kerguelen Islands. Rep. Int. Whal. Commn, Special Issue 9: 119-141.

Collet, A. and Saint Girons, H. 1984. Preliminary study of the male reproductive cycle in common dolphins, *Delphinus delphis,* in the eastern North Atlantic. Rep. Int. Whal. Commn, Special Issue 6: 355-360.

Dawson, S.M. 1985. The New Zealand whale and dolphin digest. Brick Row Publishing, Auckland.

Dawson, S.M. 1990. Sounds, acoustic behaviour and net entanglement of Hector's dolphin. PhD thesis, University of Canterbury.

Dawson, S.M. and Slooten, E. 1988. Hector's dolphin *Cephalorhynchus hectori:* Distribution and abundance. Rep. Int. Whal. Commn, Special Issue 9: 315-324.

Douglas-Hamilton, F. 1973. On the ecology and behavior of the Lake Manyara elephants. East Afr. Wildl. J. 11: 401-403.

Evans, P.G.H. 1987. The natural history of whales and dolphins. Christopher Helm Ltd, Bromley.

Finn, C.A. and Porter, D.G. 1975. The uterus. Elek Science, London.

Ford, J.K.B. 1989. Acoustic behaviour of resident killer whales *(Orcinus orca)* off Vancouver Island, British Columbia. Can. J. Zool. 67: 727-745.

Gambell, R. 1977. Dentinal layer formation in sperm whale teeth. *In* A voyage of discovery. *Edited by* M. Angel. Pergamon Press, Oxford. pp. 583-590.

Gaskin, D.E. 1982. The ecology of whales and dolphins. Heinemann Educational Books Ltd, London.

Gaskin, D.E. and Blair, B.A. 1977. Age determination of harbour porpoise, *Phocoena phocoena* (L.), in the western North Atlantic. Can. J. Zool. 55: 18-30.

Gaskin, D.E., Smith, G.J.D., Watson, A.P., Yasui, W.Y. and Yurick, D.B. 1984. Reproduction in the porpoises (Phocoenidae): Implications for management. Rep. Int. Whal. Commn, Special Issue 6: 135-148.

Gilpin, M.E. and Soulé, M.E. 1986. Minimum viable populations: Processes of species extinction. *In* Conservation biology: The science of scarcity and diversity. *Edited by* M.E. Soulé. Sinauer Associates, Sunderland. pp. 19-34.

Goodall, R.N.P. and Cameron, I.S. 1980. Exploitation of small cetaceans off southern South America. Rep. Int. Whal. Commn 30: 445-450.

Goodall, R.N.P., Galeazzi, A.R., Leatherwood, S., Miller, K.W., Cameron, I.S., Kastelein, R.K. and Sobral, A.P. 1988a. Studies of Commerson's dolphins, *Cephalorhynchus commersonii,* off Tiera del Fuego, 1976-1984, with a review of information on the species in the south Atlantic. Rep. Int. Whal. Commn, Special Issue 9: 3-70.

Goodall, R.N.P., Norris, K.S., Galeazzi, A.R., Oporto, J.A. and Cameron, I.S. 1988b. On the Chilean dolphin, *Cephalorhynchus eutropia* (Gray, 1846). Rep. Int. Whal. Commn, Special Issue 9: 197-257.

Goodman, D. 1981. Life history analysis of large mammals. *In* Dynamics of large mammal populations. *Edited by* C.W. Fowler and T.D. Smith. Wiley, New york. pp. 415-436.

Goodman, D. 1984. Statistics of reproductive rate estimates, and their implications for population projection. Rep. Int. Whal. Commn, Special Issue 6: 161-173.

Gordon, D.M. 1986. The dynamics of group behavior. *In* Perspectives in ethology. *Edited by* P.P.G. Bateson and P.H. Klopfer. Plenum Press, New York. pp. 217-231.

Gordon, D.M. 1988. Behaviour changes - finding the rules. *In* Evolutionary processes and metaphors. *Edited by* M.-W. Ho and S.W. Fox. Wiley and Sons, Chichester. pp. 243-254.

Gottman, J.M. 1980. Analyzing for sequential connection and assessing interobserver reliability for the sequential analysis of observational data. Behav. Assess. 2: 361-368.

Gough, J.D. 1988. Review of environmental impact assessment and risk assessment procedures. Unpublished report for the New Zealand Ministry for the Environment. Centre for Resource Management, University of Canterbury.

Grue, H. and Jensen, B. 1979. Review of the formation of incremental lines in tooth cementum of terrestrial mammals. Dan. Rev. Game Biol. 11: 1-48.

Gurevich, V. S., Stewart, B.S. and Cornell, L.H. 1980. The use of tetracycline in age determination of common dolphins, *Delphinus delphis*. Rep. Int. Whal. Commn, Special Issue 3: 165-169.

Hammond, P.S. 1986. Estimating the size of naturally marked whale populations using capture-recapture techniques. Rep. Int. Whal. Commn, Special Issue 8: 253-282.

Hammond, P.S., Mizroch, S.A. and Donovan, G.P. In press. Individual recognition and the estimation of cetacean population parameters. Rep. Int. Whal. Commn, Special Issue 12.

Harrison, R.J., Boice, R.C. and Brownell, R.L. Jr. 1969. Reproduction in wild and captive dolphins. Nature, Lond. 222: 1143-7.

Harrison, R.J. and Brownell, R.L. Jr. 1971. The gonads of the South American dolphins, *Inia geoffrensis, Pontoporia blainvillei* and *Sotalia fluviatilis.* J. Mammal. 52: 413-19.

Harrison, R.J., Brownell, R.L. Jr and Boice, R.C. 1972. Reproduction and gonadal appearances in some odontocetes. *In* Functional anatomy of marine mammals, Vol. 1. *Edited by* R.J. Harrison. Academic Press, London. pp. 361-429.

Harrison, R.J., Bryden, M.M., McBrearty, D.A. and Brownell, R.L. Jr. 1981. The ovaries and reproduction in *Pontoporia blainvillei* (Cetacea: Platanistidae). J. Zool. 193: 563-580.

Harrison, R.J. and Ridgway, S.H. 1971. Gonadal activity of some bottlenose dolphins *(Tursiops truncatus).* J. Zool. 165: 355-366.

Harwood, M.B. and Hembree, D. 1987. Incidental catch of small cetaceans in the offshore gillnet fishery in northern Australian waters: 1981-1985. Rep. Int. Whal. Commn 37: 363-367.

Harwood, M.B., McNamara, K.J, Anderson, G.R.V. and Walter, D.G. 1984. Incidental catch of small cetaceans in a gillnet fishery in northern Australian waters. Rep. Int. Whal. Commn 34: 555-559.

Heimlich-Boran, J.R. 1988. Behavioral ecology of killer whales *(Orcinus orca)* in the Pacific northwest. Can. J. Zool. 66: 565-578.

Helle, E., Olsson, M. and Jensen, S. 1976a. DDT and PCB levels and reproduction in ringed seal from the Bothnian Bay. Ambio 5: 188-189.

Helle, E., Olsson, M. and Jensen, S. 1976b. PCB levels correlated with pathological changes in seal uteri. Ambio 5: 261-263.

Hofman, R.J. 1990. Cetacean entanglement in fishing gear. Mammal Rev. 20(1): 53-64.

Hohn, A.A., Chivers, S.J. and Barlow, J. 1985. Reproductive maturity and seasonality of male spotted dolphins, *Stenella attenuata,* in the eastern tropical Pacific. Mar. Mamm. Sci. 1: 273-293.

Hohn, A.A., Scott, M.D., Wells, R.S., Sweeney, J.C. and Irvine, A.B. In press. Growth layers in teeth from known-age, free-ranging bottlenose dolphins. Mar. Mamm. Sci..

Horn, H.S. and Rubenstein, D.I. 1984. Behavioural adaptations and life history. *In* Behavioural ecology. An evolutionary approach. *Edited by* J.R. Krebs and N.B. Davies. Blackwell Scientific Publications, Oxford. pp. 279-303.

Irvine, A.B., Scott, M.D., Wells, R.S. and Kaufmann, J.H. 1981. Movements and activities of the Atlantic bottlenose dolphin, *Tursiops truncatus,* near Sarasota, Florida. Fish. Bull. 79: 671-688.

Jefferson, T.A. 1987. A study of the behavior of Dall's porpoise *(Phocoenoides dalli)* in the Johnstone Strait, British Columbia. Can. J. Zool. 65: 736-744.

Jones, L.L. 1984. Incidental take of the Dall's porpoise and the harbor porpoise by Japanese salmon drift net fisheries in the western North Pacific. Rep. Int. Whal. Commn 34: 531-41.

Kasuya, T. 1972. Growth and reproduction of *Stenella attenuata* based on the age determination by means of dentinal growth layers. Sci. Rep. Whales Res. Inst. Tokyo 24: 57-79.

Kasuya, T. 1976. Reconsideration of life history parameters of the spotted and striped dolphins based on cemental layers. Sci. Rep. Whales Res. Inst. Tokyo 28: 73-106.

Kasuya, T. and Brownell, R.L. Jr. 1979. Age determination, reproduction, and growth of the franciscana dolphin, *Pontoporia blainvillei.* Sci. Rep. Whales Res. Inst. Tokyo 31: 45-67.

Kasuya, T. and Marsh, H. 1984. Life history and reproductive biology of the short-finned pilot whale, *Globicephala macrorhynchus,* off the Pacific coast of Japan. Rep. Int. Whal. Commn, Special Issue 6: 259-310.

Kasuya, T., Miyazaki, N. and Dawbin, W.H. 1974. Growth and reproduction of *Stenella attenuata* in the Pacific coast of Japan. Sci. Rep. Whales Res. Inst. Tokyo 26: 157-226.

Katona, S., Baxter, B., Brazier, O., Kraus, S., Perkins, J. and Whitehead, H. 1979. Identification of humpback whales by fluke photographs. *In* Behavior of marine animals. Vol. 3: Cetaceans. *Edited by* H.E. Winn and B.L. Olla. Plenum Press, New York. pp. 33-44.

Kenagy, G.J. and Trombulak, S.C. 1986. Size and function of mammalian testes in relation to body size. J. Mammal. 67: 1-22.

Klevezal, G.A. 1980. Layers in the hard tissues of mammals as a record of growth rhythms of individuals. Rep. Int. Whal. Commn, Special Issue 3: 89-94.

Krebs, J. 1985. Sociobiology ten years on. New Sci. 3 October 1985: 40-43.

Labhsetwar, A.P. 1970. Ageing changes in pituitary-ovarian relationships. J. Reprod. Fert., Suppl. 12: 99-117.

Lande, R. 1988. Genetics and demography in biological conservation. Science 241: 1455-1460.

Leatherwood, S. and Alling, A. 1985. Marine mammals and fisheries in Sri Lanka - conflicts and possible solutions. Abstract. Sixth Biennial Conference on the Biology of Marine Mammals. Vancouver, Canada.

Leatherwood, S., Reeves, R.R., Perrin, W.F. and Evans, W.E. 1988. Whales, dolphins and porpoises of the eastern north Pacific and adjacent Arctic waters. A guide to their identification. Dover Publications Inc, New York.

Leslie, P.H. 1945. On the use of matrices in certain population mathematics. Biometrika 33: 183-212.

Leutenegger, W. and Cheverud, J.M. 1985. Sexual dimorphism in primates: The effects of size. *In* Size and scaling in primate biology. *Edited by* W.L. Jungers. Plenum Press, New York. pp. 33-50.

Liew, P.K.L. 1974. Age determination of American eels based on the structure of their otoliths. *In* Ageing of fish. Proceedings of an international symposium. *Edited by* T.B. Bagenal. Unwin Bros Ltd, England. pp.124-136.

Lockyer, C. 1984. Review of baleen whale (Mysticeti) reproduction and implications for management. Rep. Int. Whal. Commn, Special Issue 6: 27-48.

Lockyer, C. 1987. Observations on the ovary of the southern minke whale. Sci. Rep. Whales Res. Inst. Tokyo 38: 75-89.

Lockyer, C., Goodall, R.N.P. and Galeazzi, A.R. 1988. Age and body length characteristics of *Cephalorhynchus commersonii* from incidentally-caught specimens off Tierra del Fuego. Rep. Int. Whal. Commn, Special Issue 9: 103-118.

Lockyer, C. and Smellie, C.G. 1985. Assessment of reproductive status of female fin and sei whales taken off Iceland, from a histological examination of the uterine mucosa. Rep. Int. Whal. Commn 35: 343-348.

Lockyer, C., Smellie, C.G., Goodall, R.N.P. and Cameron, I.S. 1981. Examination of teeth of Commerson's dolphin *Cephalorhynchus commersonii* for age determination. J. Zool. 195: 123-131.

MacDiarmid, A.B. In press. Daily movement patterns of the spiny lobster *Jasus edwardsii* (Hutton) on a shallow reef in northern New Zealand. J. Exp. Mar. Biol. Ecol.

Mace, G.M. and Ballou, J.D. 1990. Population management for conservation. TREE 5: 102-104.

Marine Mammal Commission. 1988, 1989. Annual reports to congress. Marine Mammal Commission, Washington D.C.

Marsh, H. 1980. Age determination of the dugong (*Dugong dugon* (Müller)) in northern Australia. Rep. Int. Whal. Commn, Special Issue 3: 181-201.

Marsh, H. and Kasuya, T. 1984. Changes in the ovaries of the short-finned pilot whale *Globicephala macrorhynchus,* with age and reproductive activity. Rep. Int. Whal. Commn, Special Issue 6: 311-335.

Martin, P. and Bateson, P. 1986. Measuring behaviour. Cambridge University Press, Cambridge.

McBride, A.F. and Kritzler, H. 1951. Observations on pregnancy, parturition, and post-natal behavior in the bottlenose dolphin. J. Mammal. 32: 251-266.

Miyazaki, N. 1977. Growth and reproduction of *Stenella coeruleoalba* off the Pacific coast of Japan. Sci. Rep. Whales Res. Inst. Tokyo 29: 21-48.

Mizroch, S.A. 1983. Reproductive rates in Southern Hemisphere baleen whales. MSc thesis, University of Washington.

Mizroch, S.A. and York, A.E. 1984. Have pregnancy rates of Southern Hemisphere fin whales *Balaenoptera physalus,* increased? Rep. Int. Whal. Commn, Special Issue 6: 401-410.

Morgan, B.J.T., Simpson, M.J.A., Hanby, J.P. and Hall-Craggs, J. 1976. Visualizing interaction and sequential data in animal behaviour: Theory and application of cluster-analysis methods. Behaviour 56: 1-43.

Myrberg, A.A. and Gruber, S.H. 1974. The behaviour of the bonnethead shark, *Sphyrna tiburo.* Copeia 1974: 358-374.

Myrick, A.C. Jr, Hohn, A.A., Sloan, P.A., Kimura, M. and Stanley, D.D. 1983. Estimating age of spotted and spinner dolphins *(Stenella attenuata* and *Stenella longirostris)* from teeth. NOAA Technical Memorandum NMFS-SWFC-30. Available from Southwest Fisheries Center, P.O. Box 271, La Jolla, CA 92038, U.S.A.

Newman, D.G. 1977. Hamilton's frog. Wildl. Rev. N.Z. Wildl. Serv. 8: 48-53.

Nielsen, H.G. 1972. Age determination of the harbour porpoise *Phocoena phocoena* (L.) (Cetacea). Vidensk. Medd. Dan. Naturhist. Foren. 135: 61-84.

Norris, K.S. 1966. Standardized methods for measuring and recording data on the smaller cetaceans. J. Mammal. 42: 471-476.

Norris, K.S. and Dohl, T.P. 1980. Behavior of the Hawaiian spinner dolphin, *Stenella longirostris.* Fish. Bull. 77: 821-849.

Norris, K.S. and Schilt, C.R. 1988. Cooperative societies in three-dimensional space: On the origins of aggregations, flocks, and schools, with special reference to dolphins and fish. Ethology Sociobiol. 9: 149-179.

Norris, K.S., Würsig, B., Wells, R.S., Würsig, M., Brownlee, S.M., Johnson, C. and Solow, J. 1985. The behavior of the Hawaiian spinner dolphin, *Stenella longirostris*. NMFS Admin. Rep. LJ-85-06C.

Östman, J. In press. Changes in aggressive and homosexual behavior among two male bottlenose dolphins *(Tursiops truncatus)* in a captive colony. *In* Dolphin societies: Methods of study. *Edited by* K. Pryor and K.S. Norris. University of California Press, Berkeley.

Payne, R., Brazier, O., Dorsey, E.M., Perkins, J.S., Rowntree, V.J. and Titus, A. 1983. External features in southern right whales *(Eubalaena australis)* and their use in identifying individuals. *In* Communication and behavior of whales. *Edited by* R. Payne. AAAS Sel. Symp. 76: 371-445.

Pearce, F. 1988. Seal virus spreads to porpoises. New Sci. 5 Nov. 1988: 21.

Pennycuick, C.J. 1978. Identification using natural markings. *In* Animal marking. Recognition marking of animals in research. *Edited by* B. Stonehouse. Macmillan, London. pp. 147-159.

Perrin, W.F. (Ed.). 1987. Newsletter of the cetacean specialist group. No. 3.

Perrin, W.F. 1988. Dolphins, porpoises and whales - an action plan for the conservation of biological diversity: 1988-1992. International Union for Conservation of Nature and Natural Resources, Gland, Swizerland.

Perrin, W.F., Brownell, R.L. and DeMaster, D.P. (Eds). 1984. Reproduction in whales, dolphins and porpoises. Proceedings of the conference on cetacean reproduction: Estimating parameters for stock assessment and management. Rep. Int. Whal. Commn, Special Issue 6.

Perrin, W.F. and Donovan, G.P. (Eds). 1984. Report of the workshop. Rep. Int. Whal. Commn, Special Issue 6: 1-24.

Perrin, W.F., Holts, D.B. and Miller, R.B. 1977. Growth and reproduction of the eastern spinner dolphin, a geographical form of *Stenella longirostris* in the eastern tropical Pacific. Fish. Bull. 75: 725-750.

Perrin, W.F. and Myrick, A.C. Jr (Eds). 1980. Age determination of toothed whales and sirenians. Rep. Int. Whal. Commn, Special Issue 3.

Perrin, W.F. and Reilly, S.B. 1984. Reproductive parameters of dolphins and small whales of the family Delphinidae. Rep. Int. Whal. Commn, Special Issue 6: 97-133.

Peters, H. and McNatty, K.P. 1980. The ovary. A correlation of structure and function in mammals. Granada, London.

Petersen, J.C.B. 1972. An identification system for zebra *(Equus burchelli,* Gray). East Afr. Wildl. J. 10: 385-400.

Pryor, K. 1986. Non-acoustic communicative behavior of the great whales: Origins, comparisons, and implications for management. Rep. Int. Whal. Commn, Special Issue 8: 89-96.

Purves, P.E. and Pilleri, G. 1978. The functional anatomy and general biology of *Pseudorca crassidens* (Owen) with a review of the hydrodynamics and acoustics in Cetacea. Investigations on Cetacea 9: 67-231.

Ralls, K. 1976. Mammals in which females are larger than males. Quart. Rev. Biol. 51: 245-276.

Read, A.J. and Gaskin, D.E. 1988. Incidental catch of harbour porpoises by gill nets. J. Wild. Manage. 52: 517-523.

Read, A.J., Waerebeek, K. van, Reyes, J.C., McKinon, J.S. and Lehman, L.C. 1988. The exploitation of small cetaceans in coastal Peru. Biol. Conserv. 46: 53-70.

Reijnders, P.J.H. 1989. The cumulative role of pollution in marine mammal habitat degradation. Presented at Eighth Biennial Conference on the Biology of Marine Mammals, Pacific Grove, California.

Reilly, S.B. 1984. Observed and maximum rates of increase in gray whales, *Eschrichtius robustus.* Rep. Int. Whal. Commn, Special Issue 6: 389-399.

Reilly, S.B. and Barlow, J. 1986. Rates of increase in dolphin population size. Fish. Bull. 84: 527-533.

Rowell, T.E. 1979. How would we know if social organization were <u>not</u> adaptive? *In* Primate ecology and human origins: Ecological influences on social organization. *Edited by* I.S. Bernstein and E.O. Smith. Garland STPM Press, New York. pp. 1-22.

Rowell, T.E. and Chism, J. 1986. Sexual dimorphism and mating systems: Jumping to conclusions. Human Evolution 1: 215-219.

Rubenstein, D.I. and Wrangham, R.W. (Eds). 1986. Ecological aspects of social evolution: Birds and mammals. Princeton Uni. Press, New Jersey.

Saayman, G.S. and Tayler, C.K. 1973. Social organization of inshore dolphins *(Tursiops aduncus* and *Sousa)* in the Indian Ocean. J. Mammal. 54: 993-996.

Saayman, G.S. and Tayler, C.K. 1979. The socioecology of humpback dolphins (*Sousa* sp.). *In* Behavior of marine animals. Vol. 3: Cetaceans. *Edited by* H.E. Winn and B.L. Olla. Plenum Press, New York. pp. 165-226.

Sackett, G.P. 1979. The lag sequential analysis of contingency and cyclicity in behavioral interaction research. *In* Handbook of infant development. *Edited by* J.O. Osofsky. Wiley, New York. pp. 623-649.

Schaller, G.B. 1977. Mountain monarchs. Wild sheep and goats of the Himalaya. The University of Chicago Press, Chicago.

Schaller, G.B., Hu Jinchu, Pan Wenshi and Zhu Jing. 1985. The giant pandas of Wolong. The University of Chicago Press, Chicago.

Scheffer, V.B. and Myrick, A.C. Jr. 1980. A review of studies to 1970 of growth layers in the teeth of marine mammals. Rep. Int. Whal. Commn, Special Issue 3: 1-50.

Scott, D.K. 1978. Identification of individual Bewick's swans by bill patterns. *In* Animal marking. Recognition marking of animals in research. *Edited by* B. Stonehouse. Macmillan, London. pp. 160-168.

Scott, M.D., Wells, R.S. and Irvine, A.B. 1990. A long-term study of bottlenose dolphins on the west coast of Florida. *In* The bottlenose dolphin. *Edited by* S. Leatherwood. Academic Press, London. pp. 235-244.

Sergeant, D.E. 1959. Age determination in odontocete whales from dentinal growth layers. Norsk Hvalfangsttid. 48: 273-288.

Sergeant, D.E., Caldwell, D.K. and Caldwell, M.C. 1973. Age, growth and maturity of bottlenosed dolphin *(Tursiops truncatus)* from northeast Florida. J. Fish. Res. Board Canada 30: 1009-1011.

Setchell, B.P. 1978. The mammalian testis. Cornell University Press, Ithaca.

Shane, S.H. 1980. Occurrence, movements, and distribution of bottlenose dolphin, *Tursiops truncatus,* in southern Texas. Fish. Bull. 78: 593-601.

Shane, S.H. 1987. The behavioral ecology of the bottlenose dolphin. PhD thesis, University of California at Santa Cruz.

Shane, S.H. 1990. Behavior and ecology of the bottlenose dolphin at Sanibel Island, Florida. *In* The bottlenose dolphin. *Edited by* S. Leatherwood. Academic Press, London. pp. 245-265.

Shane, S.H., Wells, R.S. and Würsig, B. 1986. Ecology, behavior and social organization of the bottlenose dolphin: A review. Mar. Mamm. Sci. 2: 34-63.

Siegel, S. 1956. Nonparametric Statistics for the Behavioral Sciences. McGraw-Hill, New York.

Silber, G.K. 1988. Recent sightings of the Gulf of California harbor porpoise, *Phocoena sinus*. J. Mammal. 69: 430-432.

Siler, W. 1979. A competing-risk model for animal mortality. Ecology 60: 750-757.

Simberloff, D. 1988. The contribution of population and community biology to conservation science. Ann. Rev. Ecol. Syst. 19: 473-511.

Slater, P.J.B. 1973. Describing sequences of behavior. *In* Perspectives in ethology. *Edited by* P.P.G. Bateson and P.H. Klopfer. Plenum Press, New York. pp. 131-153.

Slooten, E. and Dawson, S.M. 1988. Studies on Hector's dolphin *Cephalorhynchus hectori:* A progress report. Rep. Int. Whal. Commn, Special Issue 9: 325-338.

Slooten, E. and Dawson, S.M. In press. Hector's dolphin *Cephalorhynchus hectori. In* Handbook of marine mammals. Vol. V: Delphinidae and Phocoenidae. *Edited by* S.H. Ridgway and R. Harrison. Academic Press, London.

Smith, T.D. 1983. Changes in size of three dolphin populations (*Stenella* spp.) in the eastern tropical Pacific. Fish. Bull. 81: 1-14.

Smith, T.D. and Polacheck, T. 1981. Re-examination of the life table for northern fur seals with implications about population regulatory mechnisms. *In* Dynamics of large mammal populations. *Edited by* C.W. Fowler and T.D. Smith. Wiley, New York. pp. 99-120.

Soulé, M.E. 1983. What do we really know about extinction? *In* Genetics and conservation. *Edited by* C.M. Schonewald-Cox, S.M. Chambers, B. MacBryde and W.L. Thomas. Benjamin/Cummings, Menlo Park. pp. 111-124.

Spinage, C.A. 1972. African ungulate life tables. Ecology 53: 645-652.

Tayler, C.K. and Saayman, G.S. 1972. The social organisation and behaviour of dolphins *(Tursiops aduncus)* and baboons *(Papio ursinus)* some comparisons and assessments. Ann. Cape Prov. Mus. (Nat. His.) 9(2): 11-49.

Waas, J.R. 1988. Agonistic and sexual communication in the little blue penguins, *Eudyptula minor.* PhD thesis, University of Canterbury.

Wells, R.S. 1986. Structural aspects of dolphin societies. PhD thesis, University of California at Santa Cruz.

Wells, R.S., Irvine, A.B. and Scott, M.D. 1980. The social ecology of inshore odontocetes. *In* Cetacean behavior. *Edited by* L.M. Herman. John Wiley, New York. pp. 263-317.

Wells, R.S., Scott, M.D. and Irvine, A.B. 1987. The social structure of free-ranging bottlenose dolphins. *In* Current mammalogy, Volume 1. *Edited by* H.H. Genoways. Plenum Press, New York. pp. 247-305.

Whitehead, H. 1987. Social organization of sperm whales off the Galapagos: Implications for management and conservation. Rep. Int. Whal. Commn 37: 195-199.

Whitehead, H. In press. Assessing sperm whale populations using natural markings: A progress report. Rep. Int. Whal. Commn, Special Issue 12.

Whitehead, H. and Arnbom, T. 1987. Social organization of sperm whales off the Galapagos Islands, February-April 1985. Can. J. Zool. 65: 913-919.

Würsig, B. 1978. Occurrence and group organization of Atlantic bottlenose porpoises *(Tursiops truncatus)* in an argentine bay. Biol. Bull. 154: 348-359.

Würsig, B. 1989. Cetaceans. Science 244: 1550-1557.

Würsig, B. and Jefferson, T.A. In press. Methodology of photo-identification for small cetaceans. Rep. Int. Whal. Commn, Special Issue 12.

Würsig, B. and Würsig, M. 1979. Behavior and ecology of the bottlenose dolphin, *Tursiops truncatus,* in the south Atlantic. Fish. Bull. 77: 399-413.

Würsig, B. and Würsig, M. 1980. Behavior and ecology of the dusky dolphin, *Lagenorhynchus obscurus,* in the south Atlantic. Fish. Bull. 77: 871-890.